(ISSN 0161-8202)

Journal of ARACHNOLOGY

PUBLISHED BY THE AMERICAN ARACHNOLOGICAL SOCIETY

VOLUME 39 2011 NUMBER 3

THE JOURNAL OF ARACHNOLOGY

EDITOR-IN-CHIEF: **James E. Carrel**, University of Missouri–Columbia

MANAGING EDITOR: **Douglass H. Morse**, Brown University

SUBJECT EDITORS: *Ecology*—**Stano Pekár**, Masaryk University; *Systematics*—**Mark Harvey**, Western Australian Museum and **Ingi Agnarsson,** University of Puerto Rico; *Behavior*—**Linden Higgins**, University of Vermont; *Morphology and Physiology*—**Jason Bond,** Auburn University

EDITORIAL BOARD: **Alan Cady**, Miami University (Ohio); **Jonathan Coddington**, Smithsonian Institution; **William Eberhard**, Universidad de Costa Rica; **Rosemary Gillespie**, University of California, Berkeley; **Charles Griswold**, California Academy of Sciences; **Marshal Hedin**, San Diego State University; **Herbert Levi**, Harvard University; **Brent Opell**, Virginia Polytechnic Institute & State University; **Norman Platnick**, American Museum of Natural History; **Ann Rypstra**, Miami University (Ohio); **Paul Selden**, University of Kansas; **Matthias Schaefer**, Universitæt Goettingen (Germany); **William Shear**, Hampden-Sydney College; **Petra Sierwald**, Field Museum; **I-Min Tso**, Tunghai University (Taiwan).

The *Journal of Arachnology* (ISSN 0161-8202), a publication devoted to the study of Arachnida, is published three times each year by *The American Arachnological Society*. **Memberships (yearly):** Membership is open to all those interested in Arachnida. Subscriptions to *The Journal of Arachnology* and *American Arachnology* (the newsletter), and annual meeting notices, are included with membership in the Society. Regular, $55; Students, $30; Institutional, $125. Inquiries should be directed to the Membership Secretary (see below). **Back Issues:** James Carrel, 209 Tucker Hall, Missouri University, Columbia, Missouri 65211-7400 USA. Telephone: (573) 882-3037. **Undelivered Issues:** Allen Press, Inc., 810 E. 10th Street, P.O. Box 368, Lawrence, Kansas 66044 USA.

Cover photo: Male ladybird spider, *Eresus kollari* (Eresidae), from northwest Germany. Photo by Dr. Heiko Bellmann.

Publication date: 21 December 2011

♾ **This paper meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper).**

2011. The Journal of Arachnology 39:365–377

Four new species of the genus *Pseudocellus* (Arachnida: Ricinulei: Ricinoididae) from Mexico

Alejandro Valdez-Mondragón and **Oscar F. Francke**: Colección Nacional de Arácnidos (CNAN), Departamento de Zoología, Universidad Nacional Autónoma de México (UNAM), Apartado Postal 70-153, C. P. 04510, Ciudad Universitaria, Delegación Coyoacán, Cd. de México, Distrito Federal, México. E-mail: lat_mactans@yahoo.com.mx

Abstract. Four new species of ricinuleids are described: *Pseudocellus chankin* from caves and surface collections in southern Mexico (Chiapas & Tabasco) and Guatemala (Petén); *Pseudocellus jarocho* from a single surface collection in Veracruz, México; *Pseudocellus oztotl*, a troglobitic and troglomorphic species from Cueva de Las Tres Quimeras in the Sierra Negra, Puebla, Mexico; and *Pseudocellus platnicki*, also troglobitic and troglomorphic, known from a single cave in Coahuila, Mexico. The number of known species in the genus increases to 24, and Mexican species to 14. An identification key for adult males of the species found in Mexico and southern USA is provided.

Keywords: Biodiversity, troglobites, troglomorphism, caves

The order Ricinulei is currently the smallest of Arachnida with two suborders: Paleoricinulei Selden 1992 with two families (Curculioididae Cockerell 1916 and Poliocheridae Scudder 1884), four genera and 16 fossil species; and Neoricinulei Selden 1992 with only one family (Ricinoididae Ewing 1929), three genera and 68 living species (Selden 1992; Harvey 2002, 2003; Botero-Trujillo & Pérez 2009; Tourinho & Azevedo 2007; Tourinho & Saturnino 2010; Tourinho et al. 2010). The three ricinoidid genera have distinct distributions in the world: the genus *Ricinoides* Ewing 1929 with 11 species is distributed in equatorial west and central Africa (Harvey 2003; Naskrecki 2008; Cokendolpher & Enríquez 2004; Botero-Trujillo & Pérez 2009); *Cryptocellus* Westwood 1874, with 35 species is known from Honduras southward through Central and tropical South America to Brazil (Bonaldo & Pinto-da-Rocha 2003; Harvey 2003; Pinto-da-Rocha & Bonaldo 2007; Tourinho & Azevedo 2007; Botero-Trujillo & Pérez 2008, 2009; Platnick & García 2008); and the genus *Pseudocellus* Platnick 1980, with 20 named species is distributed in North America (USA and Mexico), Cuba and Central America (Guatemala to Panama) (Gertsch & Mulaik 1939; Bolivar & Pieltain 1946; Gertsch 1971; Platnick & Pass 1982; Harvey 2003; Cokendolpher & Enríquez 2004; Teruel & Armas 2008).

Mexico has the highest diversity of ricinuleids in the world. Ten species of *Pseudocellus* are known from Mexico, not considering the four new species described in this work: *P. bolivari* (Gertsch 1971); *P. boneti* (Bolívar & Pieltain 1942); *P. gertschi* (Márquez & Conconi 1974); *P. mitchelli* Gertsch 1971; *P. osorioi* (Bolívar & Pieltain 1946); *P. pearsei* (Chamberlin & Ivie 1938); *P. pelaezi* (Coronado-Gutierrez 1970); *P. reddelli* (Gertsch 1971); *P. sbordonii* (Brignoli 1974); and *P. spinotibialis* (Goodnight & Goodnight 1952).

Ricinuleids are generally found in leaf litter and in the soil, under rocks and logs; and many of the species in the genus *Pseudocellus* inhabit caves (Cokendolpher & Enríquez 2004). Our knowledge of *Pseudocellus* in general is still very fragmentary because most of the species were originally described on the basis of few specimens or from single individuals; with few species known from male, female and immature stages (Pittard & Mitchell 1972; Platnick & Pass 1982; Cokendolpher & Enríquez 2004).

In this work four new Mexican species of *Pseudocellus* are described from the states of Chiapas, Coahuila, Puebla, and Veracruz. Two are known only from caves and are highly troglomorphic; one is known from both the surface and from two caves and shows no troglomorphisms, and the last one is known only from one location, collected under a large boulder in a pine forest, and does not have any troglomorphisms.

METHODS

The specimens, preserved in 80% ethanol, were examined and measured with a Nikon SMZ645 stereoscope. The measurements, given in mm, were made following Cooke and Shadab (1973). We named the segments of the legs following Gertsch (1971), Pittard & Mitchell (1972), and Platnick & Pass (1980) to facilitate cross-referencing. The names of copulatory structures follow Pittard & Mitchell (1972). Brief descriptions and complete measurements are provided for immature stages when available.

Dissecting microscopes (Zeiss Stemi SV11 and Nikon SMZ 800) fitted with a camera lucida were used to make the drawings. The tarsal processes and spermathecae were suspended in 96% gel alcohol (to permit proper positioning) and then covered with a thin layer of liquid ethanol (80%) to minimize diffraction during observation and drawing. The photographs of living specimens were taken with a Nikon Coolpix E4600 camera. The map was prepared with ArcView GIS Version 3.2 (Applegate 1999). Illustrations were edited with Adobe Photoshop 7.0.

The specimens are deposited primarily in the Colección Nacional de Arácnidos (CNAN) of the Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City (IBUNAM); but some are in the Colección de Arácnidos de El Colegio de la Frontera Sur (ECOSUR-ECOTAAR), Tapachula, Chiapas, México; and in the Invertebrate Zoological Collection of the Texas Memorial Museum (TMM-IZC), University of Texas, Austin. Specimens used for comparative purposes and the elaboration of the key are listed in Appendix 1. For species not included in that list, the information was obtained from the literature, primarily from the original descriptions.

Abbreviations used in the figures are: AP, accessory piece of tarsal process; LT, lamina cyathiformis of tarsomere 2; MTP, metatarsal process; S, spermathecae; TP, tarsal process.

TAXONOMY

Family Ricinoididae Ewing 1929
Genus *Pseudocellus* Platnick 1980

Pseudocellus Platnick 1980:352.

Type species.—*Cryptocellus dorotheae* Gertsch & Mulaik 1939, by original designation.

KEY TO ADULT MALES OF *PSEUDOCELLUS* SPECIES FROM MEXICO AND USA

1. Troglomorphic species with all appendages elongated (Figs. 17, 24): femur II at least 1.5× longer than carapace; tibia II longer than carapace 2
   Edaphomophic species with short appendages (Figs. 1, 10): femur II less than 1.5× carapace length; tibia II shorter than carapace 8
2. Femur II length/width ratio greater than 9; femur II over twice as long as carapace 3
   Femur II length/width ratio less than 9; femur II less than 2 × carapace length 6
3. Cheliceral fingers with 5 teeth ..... *P. reddelli*
   Cheliceral fingers with more than 5 teeth 4
4. Leg formula 2413; tibia II twice as long as patella II ..... *P. sbordonii*
   Leg formula 2431; tibia II less than two times patella length 5
5. Tibia I with a granulose prolateral hump (Figs. 24, 26); tibia II and tarsus II unarmed; body and appendages evenly, finely pitted ..... *P. platnicki* new species
   Tibia I without a granulose prolateral hump (Fig. 17); tibia II (Fig. 19) and tarsus II with two distinct rows of spines prodorsally and proventrally; body and appendages finely pitted ..... *P. oztotl* new species
6. Leg formula 2341; cheliceral fixed finger with 4 teeth; tarsal claws asymmetrical, some spatulate ..... *P. bolivari*
   Leg formula 2431; cheliceral fixed finger with 6 teeth; tarsal claws symmetrical, none spatulate 7
7. Tibia II elongated, about 11× longer than wide, with few scattered spines prolaterally; cheliceral movable finger with teeth uniform in size ..... *P. osorioi*
   Tibia II shorter, about 6× longer than wide, with two distinct rows of spines prolaterally; cheliceral movable finger with basal tooth distinctly larger than the rest ..... *P. boneti*
8. Tibia II armed with one or two distinct tubercles prolaterally 9
   Tibia II without distinct tubercles prolaterally 11
9. Femur II moderately thickened, 4× longer than wide; tibia II with a single prodorsal tubercle, lacking a distinct proventral tubercle ..... *P. pearsei*
   Femur strongly thickened, less than 2.5× longer than wide; tibia II prodorsal and proventral tubercles subequal in size .. 10
10. Femur II shorter than carapace; tibia II with prodorsal and proventral tubercles aligned, medial ..... *P. spinotibialis*
    Femur II distinctly longer than carapace; tibia II with tubercles not aligned, proventral on basal one-third, and prodorsal on distal one-third (Figs. 1, 3) ..... *P. chankin* new species
11. Leg formula 2431; carapace and opisthosoma distinctly and evenly pitted 12
    Leg formula 2341; integument not distinctly pitted 13
12. Adult 3.2 mm in total length; tibia II slightly over 0.5× carapace length; patella II and tibia II subequal in length ... *P. dorotheae*
    Adult 5.0 mm in total length; tibia II almost equal to carapace length; tibia II 1.5× longer than patella II ..... *P. mitchelli*
13. Femora I and IV conspicuously enlarged, at least 1.5× thicker than preceding and following segments ..... *P. gertschi*
    Femora I and IV not enlarged, about same thickness as preceding and following segments 14
14. Femur II thickened, 2.5× longer than wide; tibia II 1.5× or more the length of patella II ..... *P. pelaezi*
    Femur II not thickened, slightly over 4× longer than wide; tibia II 1.2× longer than patella II ..... *P. jarocho* new species

Pseudocellus chankin new species
Figs. 1–9

Pseudocellus sp. n. 2: Cokendolpher & Enriquez 2004:99.

Type material.—MEXICO: *Chiapas*: holotype male, Cueva Kolem-chen "Cueva Grande," Reserva Chan-kin, Municipio Ocosingo (16.691389°N, 90.824028°W, 144 m), 10 August 2006, A. Valdez, H. Montaño, S. Rubio, N. Pérez, I. Mondragón (CNAN-T0263). Paratypes: 1 female, same locality as holotype, 19 October 2006, A. Valdez, H. Montaño, O. Francke, A. Ballesteros (CNAN-T0280); 1 female, Hidalgo Cortés, orillas de la Reserva Montes Azules, Municipio Ocosingo (16.689194°N, 90.930167°W, 150 m), 11 August 2006, A. Valdez, H. Montaño, S. Rubio, N. Pérez, I. Mondragón (CNAN-T0281); 2 females, same locality as holotype, 7 November 2006, A. Valdez, H. Montaño, R. Paredes, G. Montiel, F. Bertoni (CNAN-T0282).

Other specimens examined.—MEXICO: *Chiapas*: 2 deutonymphs, 4 tritonymphs, same data as holotype (CNAN-Ri0001); 2 ♀♀, 1 larva, 1 tritonymph, same locality as holotype, 7 November 2006, A. Valdez, H. Montaño, R. Paredes, G. Montiel, F. Bertoni (CNAN-Ri0020). *Tabasco*: 2 ♂♂, 1 ♀, 2 larvae, Parque Estatal Agua Blanca, Ejido Las Palomas Municipio Macuspana (17.62126°N, 92.47928°W, 124 m), 12 July 2010, O. Francke, J. Cruz-López, C. Santibáñez, G. Montiel, D. Barrales, G. Contreras (CNAN-Ri0021). GUATEMALA: *Petén*: 2 ♂♂, 1 larva, 1 protonymph, Cueva del Río Murciélagos, Dos Pilas, Sayaxche, 25 March 1993, A. Cobb, B. Luke (TMM-IZC #3,288); 2 ♀♀, Kaxon Pec (Cave), Dos Pilas, Sayaxche, May 1993, A. Cobb (TMM-IZC #3,287).

Etymology.—The specific name is a noun in apposition and refers to the name of the biological reserve that includes the type locality, Reserva Chan-kin.

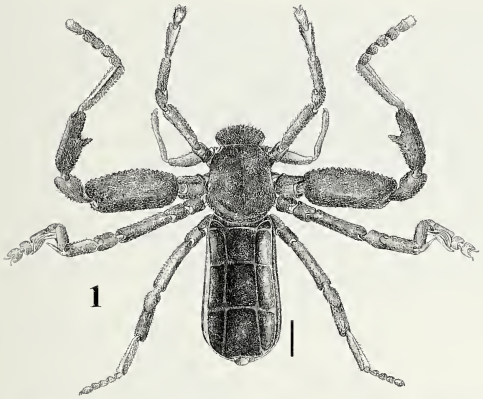


Figure 1.—*Pseudocellus chankin* new species. Male holotype. Habitus, dorsal view. Scale = 1 mm.

Diagnosis.—Males can be distinguished by the presence of two strong tubercles on tibia II, one prodorsal and the other proventral (Figs. 1, 3); by the very robust femur II (Fig. 1), 2.4 times longer than wide; by having the tarsal process curved, J-shaped (Figs. 4, 5) and the accessory piece of tarsal process of leg III (displaced position) thin, slightly curved and bifurcated distally (Fig. 5); metatarsal process conical, curved distally (Fig. 4), and cucullus trapezoidal (Fig. 2). Females can be distinguished by the curved and bifurcate spermathecae (Figs. 6, 7).

Description.—*Male (holotype):* Carapace: Slightly longer than wide, wider in posterior part near coxae III. Covered uniformly with numerous and fine translucent setae; and numerous rounded granules, more visible on marginal pale areas, located on median part, corresponding to ocular areas, between coxae I and II (Fig. 1). Dorsal depressions near to pale marginal areas, and slight depressions on posterior and median parts.

Cucullus: Wider than long, notably wider distally, with numerous rounded granules larger than those on carapace. Densely covered with long, fine translucent setae, especially on distal part, where they are also longer (Fig. 1).

Chelicerae: Fixed finger shorter than movable; fixed finger with six teeth, the distal longer and the basal one shorter; movable finger with six teeth, the basal one longer, distally decreasing in size.

Sternal region: Coxae I meeting the tritosternum in a single point; coxae II meeting it along anterior third, coxae II considerably longer than others.

Pedipalps: Trochanters 1 and 2 with few rounded granules ventrally. Femora curved distally; with few, small basal granules retrolatero-ventrally. Tibiae with granules distally on dorsal and ventral surfaces. All segments densely covered with translucent, small setae, uniform in size (Fig. 1).

Legs: Femora I–IV with numerous sharp-tipped granules ventrally, with femur II having the most. Tibiae I–II with large granules ventrally; including those on the two strong, tubercles of tibiae II (Fig. 1); tibiae III–IV with smaller granules than on I and II. Granules on metatarsi II larger than on metatarsi I. Metatarsi III-IV without granules.

Copulatory apparatus: Metatarsus short and wide, conical; tarsal process wider in distal half (Figs. 4, 5). Tarsomere 1 curved ventrally. Lamina cyathiformis of tarsomere 2 with slight notch basally; tarsomere 2 rectangular (Fig. 4).

Opisthosoma: Longer than wide, widest at posterior part, near tergite XIII (Fig. 1). Tergite XI as wide as long, tergites XII–XIII and lateral tergites longer than wide (Fig. 1). Lateral tergites in diagonal position, forming an ample concavity in median part (Fig. 1). Covered uniformly with numerous, small translucent setae both dorsally and ventrally, and without granules. Pygidium basal segment without notch on posterior dorsal and ventral margins.

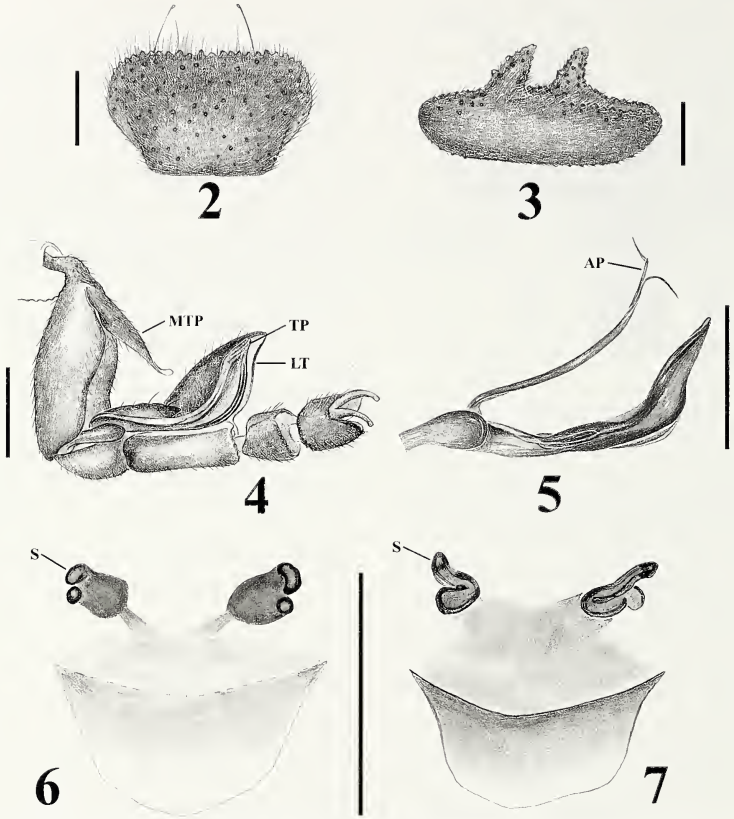
Coloration: Appendages and body reddish brown. Pedipalps lighter than other appendages; all appendages lighter red distally. Cucullus, carapace, opisthosoma and legs II dark reddish, legs II darker reddish than other appendages. Opisthosoma ventrally with dark region covering ¾ of its length.

Measurements: Total length (carapace + opisthosoma + pygidium) 6.15. Carapace 2.10 long, 1.95 wide (widest part). Cucullus 0.87 long, 1.42 wide. Opisthosoma 4.25 long, 2.20 wide (widest part). Robustness of leg II, ratio of male femur II: length / diameter (widest part) (femur II l/d): 2.37. Legs tarsal formula (legs I–IV): 1-5-4-5. Leg lengths, I: coxa 0.86/ trochanter 1 0.56/ trochanter 2 -/ femur 1.58/ patella 0.75/ tibia 1.15/ metatarsus 1.28/ tarsus 0.62/ total 6.80; II: 1.16/ 0.87/ -/ 2.87/ 1.23/ 2.00/ 1.85/ 2.2/ 12.18; III: 0.92/ 0.60/ 0.62/ 1.52/ 0.80/ 0.98/ 1.10/ 1.60/ 8.14; IV: 0.81/ 0.63/ 0.58/ 1.73/ 0.80/ 1.12/ 1.13/ 1.33/ 8.13; Pedipalp: 0.7/ 0.8/ 0.45/ 1.13/ -/ 1.60/ -/ 0.14/ 4.82. Leg formula: 2341.

Variation (n = 5): One male from Petén dark red, holotype and the other male from Petén lighter in color. Males from Tabasco lighter red than the others. Granules larger and more visible on males from Petén and Tabasco than on the other two males, especially on all segments of leg II. Movable finger of chelicerae with six teeth on the holotype, on one male from Petén and on one male from Tabasco; seven teeth on the other male from Petén; and five teeth on the other male from Tabasco. The two ventral tubercles on tibia II thinner and smaller on one male from Petén and males from Tabasco than on the other two males. Total length: 6.15–6.80 ($\bar{x}$ = 6.40 ± 0.32), Cucullus: width 1.45–1.60 ($\bar{x}$ = 1.56 ± 0.10), Carapace: width 1.95–2.10 ($\bar{x}$ = 2.00 ± 0.07), Opisthosoma: length 4.25–5.00 ($\bar{x}$ = 4.50 ± 0.38), width 2.20–2.45 ($\bar{x}$ = 2.35 ± 0.13). Femur II l/d: 2.27–2.80 ($\bar{x}$ = 2.53 ± 0.21).

Female (paratype): Differs from male as follows: Femur II not as robust, 3.7 times longer than wide. Left fixed finger of chelicerae with four teeth, right with five teeth. Femora I-IV with fewer and smaller ventral sharp-tipped granules than the male. Tibiae II with the two prolateral tubercles smaller than on the male. Tibiae III–IV with fewer granules. Opisthosoma wider than on the male. Tergite XI wider than long. Tergite XII as wide as long. Opisthosoma ventrally with two dark thin depressions, on sternites XI, XII and XIII.

Measurements: Total length 6.35. Carapace length 2.15, width 2.10 (widest part). Cucullus length 0.90, width 1.47. Opisthosoma length 4.50, width 2.75 (widest part). Femur II l/d: 3.50. Legs tarsal formula (legs I–IV): 1-5-4-5. Leg lengths, I:



Figures 2–7.—*Pseudocellus chankin* new species. Male holotype. 2. Cucullus, dorsal view; 3. Left tibia II, ventral view; 4. Left leg III, metatarsus and tarsal process, prolateral view; 5. Tarsal process (displaced position), prolateral view. Female paratype. Spermathecae; 6. Anterior view; 7. Posterior view. Scales = 0.5 mm.

coxae 0.92/ trochanter 1 0.50/ trochanter 2 -/ femur 1.45/ patella 0.70/ tibia 1.05/ metatarsus 1.23/ tarsus 0.66/ total 6.51; II: 1.15/ 0.77/ -/ 2.57/ 1.05/ 1.80/ 1.87/ 2.12/ 11.33; III: 0.93/ 0.53/ 0.66/ 1.58/ 0.78/ 1.00/ 1.10/ 1.00/ 7.58; IV: 0.86/ 0.55/ 0.56/ 1.71/ 0.72/ 1.10/ 1.15/ 1.10/ 7.75; Pedipalp: 0.75/0.38/ 0.46/ 1.12/ -/ 1.65/ -/ 0.16/ 4.52. Leg formula: 2431.

Variation (n = 7): Five females are dark reddish (two from Chiapas, two from Petén, and the female from Tabasco), and the other two females from Chiapas are lighter. Body granulation more conspicuous on lighter specimens. Chelicerae with a variable number of teeth, females from Chiapas: 1) fixed finger 4/ movable finger 6; 2) 6/8; 3) 5/7; 4) 5/6; females from Petén: 1) 5/6; 2) 5/7. Total length: 6.00–7.15 ($\bar{x}$ = 6.45 ± 0.43), Cucullus: width 1.42–1.67 ($\bar{x}$ = 1.54 ± 0.10), Carapace: width 1.95–2.25 ($\bar{x}$ = 2.09 ± 0.11), Opisthosoma: length 4.15–4.90 ($\bar{x}$ = 4.45 ± 0.30), width 2.60–2.95 ($\bar{x}$ = 2.72 ± 0.13). Femur II l/d: 3.50–3.86 ($\bar{x}$ = 3.72 ± 0.15).

Larva: Carapace wider than long, with numerous small rounded granules. Cucullus wider than long, with a small concavity distally, covered with numerous and fine translucent setae, longer distally. Legs with numerous small granules and abundant fine translucent setae. Opisthosoma slightly longer than wide, covered with numerous small rounded granules and translucent setae; tergites XI–XIII wider than long; sternites XI–XIII well visible and not fused in comparison with adults. Appendages and body coloration pale brown; paler in cucullus and carapace. Measurements: Total length 1.87. Carapace 0.86 long, 0.95 wide (widest part). Cucullus 0.40 long, 0.66 wide. Opisthosoma 1.28 long, 1.22 wide. Legs tarsal formula (legs I–III) (larva hexapod): 1-2-2. Variation: (n = 4). Total length 1.87–2.70 ($\bar{x}$ = 2.28 ± 0.58). Cucullus: width 0.65–0.66 ($\bar{x}$ = 0.655 ± 0.007), Carapace: width 0.93–0.95 ($\bar{x}$ = 0.94 ± 0.01), Opisthosoma: long 1.28–1.66 ($\bar{x}$ = 1.47 ± 0.26), wide 1.22–1.33 ($\bar{x}$ = 1.27 ± 0.07).

Figures 8–9.—*Pseudocellus chankin* new species. 8. Male holotype walking on the ground inside the cave; 9. Female paratype walking on a wall inside the cave. (Photos by Alejandro Valdez-Mondragón).

Protonymph: Carapace longer than wide. Carapace, cucullus, legs and opisthosoma covered with numerous rounded granules and translucent setae like the larva. Cucullus wider than long; with fine translucent setae longer distally, like the larva. Opisthosoma longer than wide, tergites XI–XIII wider than long; sternites XI–XIII visible like the larva, and not fused like on the adults. Appendages and body coloration brown, darker than the larva, but not as dark as adults. Measurements: Total length 3.25. Carapace 1.16 long, 1.13 wide (widest part). Cucullus 0.50 long, 0.77 wide. Opisthosoma 2.05 long, 1.60 wide. Legs tarsal formula (legs I–IV): 1-4-3-2.

Deutonymph: Carapace slightly longer than wide. Carapace, cucullus, legs and opisthosoma covered with numerous rounded granules and translucent setae like the previous life stages. Cucullus wider than longer; with fine translucent setae, longer distally, like the previous life stages. Opisthosoma longer than wide, tergites XI and XII wider than long, tergite XIII slightly longer than wide; sternites XI–XIII well visible and not fused in comparison to adults. Appendages and body coloration brown, opisthosoma brown darker than cucullus, carapace and appendages. Measurements: Total length 4.40. Carapace 1.37 long, 1.35 wide (widest part). Cucullus 0.61 long, 1.00 wide. Opisthosoma 2.80 long, 1.90 wide. Legs tarsal formula (legs I–IV): 1-5-4-4. Variation: (n = 2). One specimen with brown coloration paler than the other. Total length 4.40, 4.65 ($\bar{x}$ = 4.52). Cucullus: width 1.00, 1.00 ($\bar{x}$ = 1.00), Carapace: width 1.35, 1.40 ($\bar{x}$ = 1.37), Opisthosoma: long 2.80, 3.00 ($\bar{x}$ = 2.90), wide 1.90, 2.10 ($\bar{x}$ = 2.00).

Tritonymph: Carapace slightly longer than wide, with two dorsal depressions on median part (one on each side) and four on posterior part (two on each side). Carapace, cucullus, legs, and opisthosoma covered with numerous rounded granules and translucent setae as in the previous life stages. Cucullus wider than long, with numerous fine translucent setae, longer distally, as in previous stages. Opisthosoma longer than wide, tergites XI and XII wider than long, tergite XIII longer than wide; sternites XI–XIII well visible, not fused together in comparison with adults. Appendages and body orange-brown, paler than adults. Measurements: Total length 5.95. Carapace 1.70 long, 1.65 wide (widest part). Cucullus 0.75 long, 1.22 wide. Opisthosoma 3.90 long, 2.45 wide. Legs tarsal formula (legs I–IV): 1-5-4-5. Variation: (n = 4). Two specimens orange-brown coloration, the other two specimens lighter. Total length 5.35–5.95 ($\bar{x}$ = 5.66 ± 0.24). Cucullus: width 1.15–1.22 ($\bar{x}$ = 1.17 ± 0.03), Carapace: width 1.65–1.70 ($\bar{x}$ = 1.66 ± 0.02), Opisthosoma: long 3.75–3.90 ($\bar{x}$ = 3.85 ± 0.07), wide 2.45–2.55 ($\bar{x}$ = 2.50 ± 0.05).

Related species.—*Pseudocellus chankin* resembles *Pseudocellus seacus* Platnick & Pass 1982 from Finca Seacté, near Cobán, Alta Verapaz, Guatemala, by having the similar shape of the two large tubercles of tibia II, but on *P. chankin* these tubercles are larger than on *P. seacus*; on *P. seacus* both of these tubercles are aligned, on the basal one-third of the tibia, whereas on *P. chankin* they are offset; one is dorsomedian and the other one ventrodistal (Fig. 3). *Pseudocellus chankin* has very robust femur II, approximately 2.4 times longer than wide, whereas on *P. seacus* it is relatively thinner, "about three times as long as wide" (Platnick & Pass 1982:5). There is a considerable difference in size, the new species larger: the total length of male holotype of *P. chankin* is 6.15 mm, whereas the total length of the male of *P. seacus* is only 3.67 mm. In addition, the tarsal process of the copulatory apparatus on *P. seacus* is trifurcated distally, whereas on *P. chankin* it is wider distally and is conical-shaped with a single, blunt end (Figs. 4, 5); the accessory piece on *P. chankin* is bifurcated distally, whereas on *P. seacus* it is not. The metatarsal process in the new species is longer, about two-thirds the length of the metatarsus, whereas on *P. seacus* it is only about one-third the length of the metatarsus. Finally, the spermathecae are similar in both species, but on the new species they are thinner than on *P. seacus* (Figs. 6, 7).

Distribution.—This species is known from Chiapas and Tabasco in Mexico, and Petén in Guatemala (Fig. 31).

Natural history.—Specimens of *P. chankin* from Chiapas were collected at 144 m elev., deep inside the cave, except the female from Hidalgo Cortés which was collected under a rock in the tropical rainforest of the Reserva de Montes Azules. The specimens from the cave were collected approximately 50 m inside it, on the walls and under rocks, near bat guano (Figs. 8, 9). The cave had high humidity, ca 70%, and was fairly warm. The habitat outside the cave is tropical rainforest, in the Lacandona region located in eastern Chiapas, near the border with Guatemala.

Remarks.—Cokendolpher & Enríquez (2004) reported the specimens from Guatemala (see Other Specimens Examined,

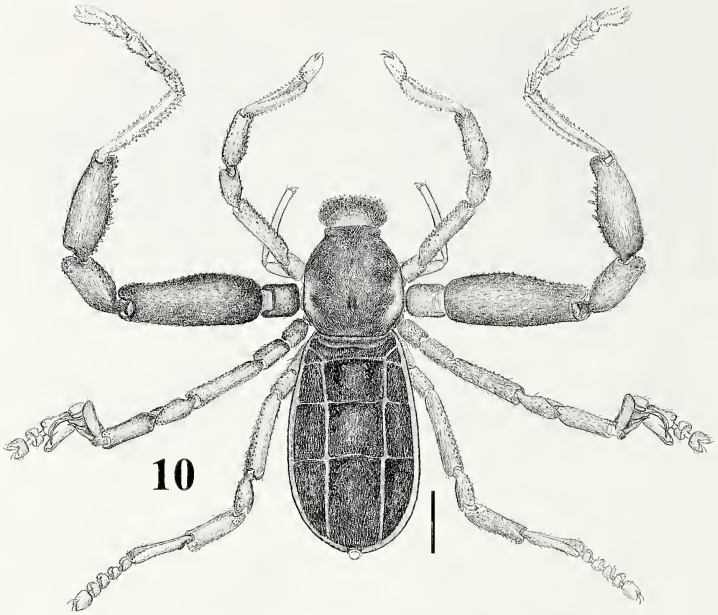


Figure 10.—*Pseudocellus jarocho* new species. Male holotype. Habitus, dorsal view. Scale = 1 mm.

above) as a new species of *Pseudocellus*, but the species was not described.

Pseudocellus jarocho new species
Figs. 10–16

Type material.—MEXICO: *Veracruz*: holotype male, 5 km E of Tlaquilpa (18.64103333°N, 97.10725°W, 2169 m), 24 March 2007, A. Valdez, O. Francke, H. Montaño, C. Santibáñez, A. Ballesteros, pine-oak forest (CNAN-T0627). Paratypes: 1 female (CNAN-T0628), 1 male, 2 females, 2 tritonymphs (CNAN-T0629), same data as holotype.

Etymology.—The specific name is a noun in apposition and refers to the common name given to people born in the state of Veracruz: Jarocho.

Diagnosis.—Males can be distinguished by the two ventral rows of curved spines on tibia II (Fig. 12); by having tarsal process with two tips distally, and the accessory piece of tarsal process of leg III (displaced position) bifurcated (Fig. 14); metatarsal process relatively long and curved (Fig. 13); and by the evenly oval shape of the cucullus (Fig. 11). Females can be distinguished by the double receptacle of the spermathecae in each side, and rounded distally (Figs. 15, 16).

Description.—*Male (holotype):* Carapace: Slightly longer than wide, wider posteriorly, at level of coxae II and III. Covered with numerous, long, fine translucent setae; and numerous, small round granules, visible on ocular areas or marginal pale areas, located near coxae II (Fig. 10). Dorsal depression shallow, longitudinal, medial.

Cucullus: Wider than long, rounded laterally, with a slight notch distally. With numerous small, round granules; with moderately dense, fine and long translucent setae, especially on distal part where they are longer (Fig. 11).

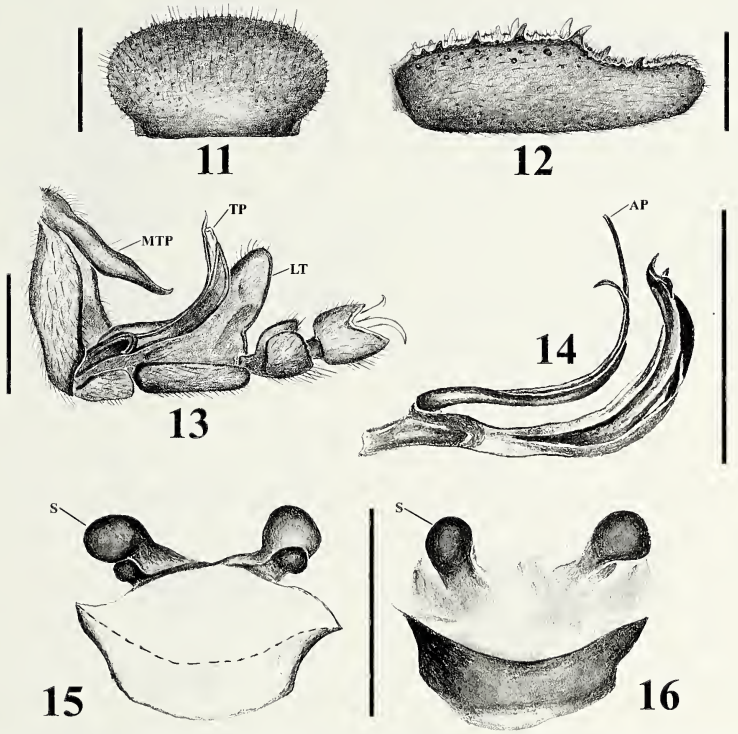
Chelicerae: Fixed finger shorter than movable, right fixed finger with six teeth, left with five, increasing in size distally. Both movable fingers with six teeth, basal-most longest.

Sternal region: Coxae I meeting the tritosternum in a single point; coxae II meeting it along anterior quarter, coxae II longer than others.

Pedipalps: Trochanters 1 and 2 with few ventral rounded granules. Femora curved distally; without granules; with fine, translucent setae, distally decreasing in size. Tibiae with rounded granules ventro-distally; with fine, translucent setae, mostly uniform in size but some longer ones distally.

Legs: Femora I, III and IV with two ventral rows of spines. Femur II with dispersed ventral spines. Tibia I with two ventral rows of small spines. Tibia II with two ventral rows of large spines (Fig. 12). Tibiae III–IV with few spines. Metatarsus I with two dorsal rows of spines, ventrally with dispersed granules. Metatarsus II with numerous prolateral, retrolateral, and ventral spines, and with two ventral rows of spines, shorter than on tibia II. Metatarsus IV distally with two dorsal rows with few spines, ventrally without granules.

Copulatory apparatus: Metatarsus short and wide, ventrally with one slight notch distally. Metatarsal process long and sigmoidal; tarsal process curved, widest at ¾ of its length (Fig. 13). Lamina cyathiformis of tarsomere 2 rounded



Figures 11–16.—*Pseudocellus jarocho* new species. Male holotype. 11. Cucullus, dorsal view; 12. Left tibia II, dorsal view; 13. Left leg III, metatarsus and tarsal process, prolateral view; 14. Tarsal process (displaced position), prolateral view. Female paratype. Spermathecae; 15. Anterior view; 16. Posterior view. Scales = 0.5 mm (Figs. 11–14), 0.3 mm (Figs. 15, 16).

distally, with slight notch basally; tarsomere 2 wider basally than distally (Fig. 13).

Opisthosoma: Longer than wide, widest at posterior part, between tergites XII and XIII (Fig. 10). Tergite XI wider than long, tergites XII–XIII and lateral tergites longer than wide (Fig. 10). Lateral tergites inclined up and outwards, forming an ample concavity in median region (Fig. 10). Ventrally and dorsally covered uniformly with numerous fine, translucent setae. Tergites X–XIII with granules, vestigial on tergite XIII. Pygidium basal segment without notches posteriorly on dorsal and ventral margins.

Coloration: Body reddish-brown; pedipalps, legs I, III–IV dark brown, lighter distally. Cucullus, carapace, opisthosoma and legs II dark reddish. Opisthosoma dark ventrally.

Measurements: Total length (carapace + opisthosoma + pygidium) 5.15. Carapace 1.70 long, 1.60 wide (widest part). Cucullus 0.73 long, 1.15 wide. Opisthosoma 3.42 long, 2.05 wide (widest part). Femur II l/d: 2.58. Legs tarsal formula (legs I–IV): 1-5-4-5. Leg lengths, I: coxa 0.80/ trochanter 1 0.48/ trochanter 2 -/ femur 1.37/ patella 0.62/ tibia 1.00/ metatarsus 1.17/ tarsus 0.52/ total 5.96; II: 0.97/ 0.72/ -/ 2.27/ 1.10/ 1.67/ 1.62/ 1.90/ 10.25; III: 0.76/ 0.51/ 0.55/ 1.38/ 0.73/ 0.86/ 0.90/ 1.42/ 7.11; IV: 0.70/ 0.57/ 0.53/ 1.45/ 0.65/ 1.00/ 1.01/ 1.07/ 6.98. Pedipalp: 0.55/ 0.32/ 0.30/ 0.93/ -/ 1.37/ -/ 0.15/ 3.62. Leg formula: 2341.

Variation: (n = 2). Paratype male reddish-brown, darker than holotype. Granules on body and legs more developed on holotype than on paratype. Movable finger of chelicerae with six teeth on holotype, five teeth on paratype. The number of long spines on the two ventral rows on tibia II variable but similar in shape on both males. The number of spines on the two ventral rows on metatarsus II variable and longer on the holotype than on the paratype. Total length: 5.10, 5.15 ($\bar{x}$ = 5.12), Cucullus: width 1.13, 1.15 ($\bar{x}$ = 1.14), Carapace: width 1.55, 1.60 ($\bar{x}$ = 1.57), Opisthosoma: length 3.37, 3.42 ($\bar{x}$ = 3.39), width 1.92, 2.05 ($\bar{x}$ = 1.98), Femur II l/d: 2.58, 3.14 ($\bar{x}$ = 2.86).

Female (paratype): Differs from male as follows: Cheliceral right fixed finger with six teeth, left with nine teeth. Femur II with dispersed ventral spine-shaped granules, faint. Tibia II with two ventral rows of spines smaller than on the male.

Metatarsus I with ventral dispersed granules, only basally. Numerous prolateral, retrolateral, and ventral spine-shaped granules, and the two ventral rows of spines of metatarsus II smaller than the male. Opisthosoma ventrally lighter than on the male.

Measurements: Total length 5.40. Carapace 1.72 long, 1.70 wide (widest part). Cucullus 0.73 long, 1.20 wide. Opisthosoma 3.70 long, 2.20 wide (widest part). Femur II l/d: 4.10. Legs tarsal formula (legs I–IV): 1-5-4-5. Leg lengths, I: coxa 0.75/ trochanter I 0.46/ trochanter II -/ femur 1.28/ patella 0.60/ tibia 0.93/ metatarsus 1.16/ tarsus 0.53/ total 5.71; II: 1.00/ 0.71/ -/ 2.05/ 0.96/ 1.60/ 1.63/ 1.83/ 9.78; III: 0.85/ 0.50/ 0.50/ 1.35/ 0.68/ 0.98/ 1.00/ 0.90/ 6.76; IV: 0.73/ 0.58/ 0.53/ 1.41/ 0.67/ 1.06/ 1.05/ 1.02/ 7.05; Pedipalp: 0.62/0.38/ 0.42/ 1.02/ -/ 1.51/ -/ 0.15/ 4.10. Leg formula: 2431.

Variation: (n = 2). One female reddish, darker than the other one. Granules more prominent on lighter female. Variable number of ventral spine-shaped tubercles on femur II. Variable number and size of spines on ventral rows of tibia and metatarsus II. Total length: 5.25, 5.40 ($\bar{x}$ = 5.32), Cucullus: width 1.15, 1.20 ($\bar{x}$ = 1.17), Carapace: width 1.62, 1.70 ($\bar{x}$ = 1.66), Opisthosoma: length 3.60, 3.70 ($\bar{x}$ = 3.65), width 2.10, 2.20 ($\bar{x}$ = 2.15). Femur II l/d: 4.10, 4.60 ($\bar{x}$ = 4.35).

Tritonymph: Carapace as long as wide, with two inconspicuous dorsal depressions on median part (one on each side) and four inconspicuous on posterior part (two on each side). Carapace, cucullus, legs, and opisthosoma covered with numerous rounded granules and translucent setae. Cucullus wider than long, covered with fine translucent setae, longer distally. Opisthosoma longer than wide, tergites XI and XII wider than long, tergite XIII longer than wide; sternites XI–XIII well visible, not fused in comparison with adults. Appendages and body brown-orange, darker on opisthosoma. Measurements: Total length 5.00. Carapace 1.45 long, 1.45 wide (widest part). Cucullus 0.61 long, 1.00 wide. Opisthosoma 3.32 long, 2.22 wide. Legs tarsal formula (legs I–IV): 1-5-4-5. Variation: (n = 2). One specimen orange-brown in color, the other brown. Total length 4.25, 5.00 ($\bar{x}$ = 4.62). Cucullus: width 1.00, 1.00 ($\bar{x}$ = 1.00); Carapace: width 1.45, 1.45 ($\bar{x}$ = 1.45); Opisthosoma: length 3.32, 2.97 ($\bar{x}$ = 3.14); width 2.22, 1.95 ($\bar{x}$ = 2.08).

Related species.—*Pseudocellus jarocho* resembles *Pseudocellus dorotheae* from Edinburg, Texas, USA, and *P. pelaezi* from San Luis Potosí, Mexico. The resemblance with *P. dorotheae* is in the similar overall shape and in the ventral spines of patella and tibia II, but on *P. jarocho* the patella is convex ventrally, whereas on *P. dorotheae* it has a deep medial concavity; *P. dorotheae* has patella II longer than *P. jarocho*, with larger spines, particularly distally; *P. jarocho* has the spines along the two ventral rows of the tibia II larger than on *P. dorotheae* (Fig. 12), and that species has more spines than *P. jarocho*. Tibia II of *P. jarocho* has a distal concavity deeper than *P. dorotheae* (Fig. 12). The new species is larger: the total length of holotype male of *P. jarocho* is 5.15 mm, whereas the male of *P. dorotheae* is 3.15 mm long. Metatarsus III is proportionally two times slightly longer on *P. jarocho* than on *P. dorotheae*, and the metatarsal process in that species is curved, whereas on *P. jarocho* it is sigmoidal (Fig. 13). Finally, the tarsal process on *P. dorotheae* is S-shaped whereas on *P. jarocho* it is J-shaped (Figs. 13, 14).

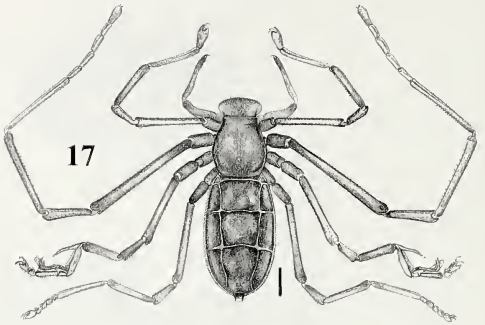


Figure 17.—*Pseudocellus oztotl* new species. Male holotype. Habitus, dorsal view. Scale = 1 mm.

The resemblance with *P. pelaezi* is in the similar shape of tibia II and in the two ventral rows of spines of tibia II, but on *P. jarocho* tibia II has a distal concavity deeper than *P. pelaezi* and the two ventral rows of spines are longer and stronger than on *P. pelaezi* (Figs. 10, 12). *Pseudocellus jarocho* is larger than *P. pelaezi*: total length of holotype male is 5.15 mm, whereas the male of *P. pelaezi* has a total length of 3.90 mm. *Pseudocellus jarocho* has femur and patellae II stronger than *P. pelaezi* (Fig. 10), although the patellae II of *P. pelaezi* has more granules ventrally than *P. jarocho*. *Pseudocellus jarocho* has two dorsal rows of strong spines on metatarsus II (Fig. 10), while *P. pelaezi* has only numerous dorsal granules, not distinctly aligned. *Pseudocellus jarocho* has small spines dorsally on tarsomeres I–III of tarsus II (Fig. 10), while *P. pelaezi* has small dorsal granules on these tarsomeres. Finally, *Pseudocellus jarocho* has metatarsus III of male longer than on *P. pelaezi*, and also *P. jarocho* has the metatarsal process thinner than on *P. pelaezi* (Fig. 13).

Distribution.—This species is known only from the type locality (Fig. 31).

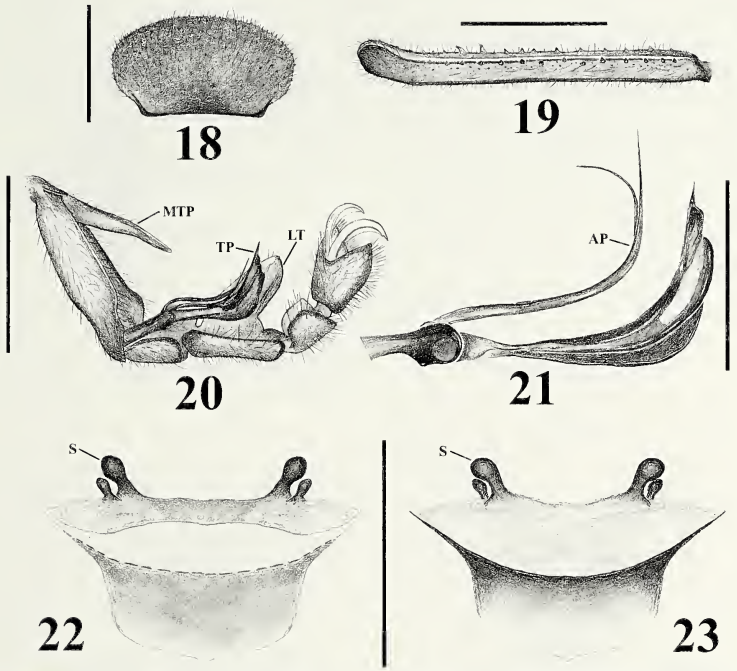
Natural history.—All specimens of *P. jarocho* were collected under the same boulder, around 80 cm in diameter. The type locality is in pine-oak forest, located in an extensive karstic zone with many rocks and boulders, 2,169 m elev.

Pseudocellus oztotl new species
Figs. 17–23

Type material.—MEXICO: *Puebla*: holotype male, from "Cueva de Las Tres Quimeras" (18.31168°N, 96.84589°W), Tlacotepec de Díaz, Municipio de San Sebastián Tlacotepec, 1 April 2009, B. Shade (CNAN-T0680). Paratypes: 1 female (CNAN-T0681), 1 male (CNAN-T0682), same data as holotype.

Etymology.—The specific name is a noun in apposition, and refers to their cave habitat, *'oztotl'* means *'cave'* in the Nahuatl language, an ancient language currently spoken by some native people from Central Mexico, including the State of Puebla and the mountainous region around the type locality.

Diagnosis.—Troglomorphic, pale and elongated: femur II 11 times longer than wide on males (Fig. 17), 12.5 times on female. Males can be distinguished by the two ventral rows of



Figures 18–23.—*Pseudocellus oztoil* new species. Male holotype. 18. Cucullus, dorsal view; 19. Left tibia II, dorsal view; 20. Left leg III, metatarsus and tarsal process, prolateral view; 21. Tarsal process (displaced position), prolateral view. Female paratype. Spermathecae; 22. Anterior view; 23. Posterior view. Scales = 1 mm (Figs. 18–20), 0.5 mm (Figs. 21–23).

short spines on the thin tibiae II (Fig. 19); the tarsal process wider distally and evenly curved (Fig. 21); by the distally bifurcated accessory piece of the tarsal process (displaced position) and by the shape of cucullus (Fig. 18). Females can be distinguished by the small and double rounded spermathecae (Figs. 22, 23).

Description.—*Male (holotype):* Carapace: Longer than wide, noticeably wider posteriorly, near coxae IV; covered with numerous, long, translucent setae (Fig. 17). Median longitudinal groove distinct; dorsal concavity point-shaped, located in posterior part of longitudinal groove (Fig. 17). With four inconspicuous marginal depressions.

Cucullus: Wider than long, with numerous rounded granules, larger than those on carapace. Long translucent setae, increasing in size distally (Fig. 18).

Chelicerae: Fixed finger shorter than movable; fixed finger with six teeth, distal tooth longer than others; movable finger with seven teeth, basal tooth longer than others.

Sternal region: Coxae I meet the tritosternum distally; coxae II meet it along anterior fourth; coxae II considerably longer and wider than others.

Pedipalps: Trochanter 1 with numerous rounded granules, trochanter 2 with rounded granules ventrodistally. Femur curved distally, without rounded granules. Tibia with few, rounded granules ventrodistally. Femur and tibia with numerous translucent setae; on femur longer ventrally, on tibia longer distally.

Legs: Femora I–IV with few ventral spines. Femur II wider than others (Fig. 17). Tibia I and II with few ventral spines, longer in tibia II (Fig. 19). Tibia III and IV without spines. Metatarsus I with few dorsal spines. Metatarsus II with numerous ventral spines. Metatarsus III without granules, metatarsus IV with few dorsal spines distally.

Copulatory apparatus: Metatarsus with metatarsal process long (Fig. 20). Tarsal process wide and curved (Figs. 20, 21). Lamina cyathiformis of tarsomere 2 with slight notch basally (Fig. 20).

Opisthosoma: Longer than wide (Fig. 17). Covered uniformly with numerous, small translucent setae dorsal and ventrally. Tergites XI and XII wider than long, tergite XIII longer than wide (Fig. 17). Lateral tergites longer than wide (Fig. 17). All tergites with numerous small, rounded granules. Tergites XI–XIII with paired shallow concavities.

Coloration: Cucullus, carapace, and opisthosoma brownish, opisthosoma darker. Pedipalps and legs light brown, legs II darker. Tarsomeres on all legs pale brown.

Measurements: Total length (carapace + opisthosoma + pygidium) 6.70. Carapace 2.00 long, 1.90 wide (widest part). Cucullus 1.00 long, 1.63 wide. Opisthosoma 4.70 long, 2.66 wide (widest part). Femur II l/d: 10.25. Legs tarsal formula (legs I–IV): 1-5-4-5. Leg lengths, I: coxa 0.98/ trochanter 1 0.65/ trochanter 2 -/ femur 2.50/ patella 1.05/ tibia 1.75/ metatarsus 2.00/ tarsus 0.82/ total 9.75; II: 1.05/ 1.00 / -/ 4.10/ 1.95/ 3.00/ 3.05/ 3.25/ 17.40; III: 0.90/ 0.80/ 0.95/ 2.55/ 1.10 / 1.50/ 1.27/ 1.65/ 10.72; IV: 0.80/ 0.83/ 0.86/ 2.85/ 1.16/ 1.95/ 1.70/ 1.55/ 11.70; Pedipalp: 0.83/ 0.50/ 0.45/ 1.28/ -/ 1.88/ -/ 0.23/ 5.17. Leg formula: 2431.

Variation: (n = 2). Holotype male darker than paratype. Paired concavities on tergites XI-XIII less inconspicuous on paratype than on holotype. Total length: 6.40, 6.70 ($\bar{x}$ = 6.55), Cucullus: width 1.55, 1.63 ($\bar{x}$ = 1.59), Carapace: width 1.85, 1.90 ($\bar{x}$ = 1.87), Opisthosoma: length 4.70, 4.71 ($\bar{x}$ = 4.705), width 2.57, 2.66 ($\bar{x}$ = 2.61). Femur II l/d: 10.25, 10.75 ($\bar{x}$ = 10.50).

Female (paratype): Differs from male as follows: Femora I–IV with fewer and smaller ventral spines. Tibiae I, III–IV without ventral spines. Tibiae II with fewer and smaller ventral spines. Sternites XI, XII and XIII with paired dark, thin depressions.

Measurements: Total length 6.50. Carapace 1.90 long, 1.85 wide (widest part). Cucullus 0.96 long, 1.53 wide. Opisthosoma 4.80 long, 2.87 wide (widest part). Femur II l/d: 11.42. Legs tarsal formula (legs I–IV): 1-5-4-5. Leg lengths, I: coxa 0.95/ trochanter 1 0.63/ trochanter 2 -/ femur 2.45/ patella 0.97/ tibia 1.80/ metatarsus 1.92/ tarsus 0.76/ total 9.48; II: 1.08/ 0.95/ -/ 3.97/ 1.77/ 2.90/ 3.03/ 2.95/ 16.65; III: 0.90/ 0.75/ 0.86/ 2.73/ 1.10 / 1.82/ 1.60/ 1.26/ 11.02; IV: 0.83/ 0.85/ 0.85/ 2.86/ 1.11/ 1.92/ 1.78/ 1.38/ 11.58; Pedipalp: 0.83/0.47/ 0.43/ 1.33/ -/ 1.91/ -/ 0.26/ 5.23. Leg formula: 2431.

Related species.—*Pseudocellus oztotl* resembles *P. osorioi* from Cueva de Los Sabinos, San Luis Potosí, México, and the other new troglomorphic species described below (see discussion in the descriptions of those species below). *Pseudocellus oztotl* is longer than *P. osorioi*: the total length (carapace + opisthosoma + pygidium) of *P. oztotl* is 6.55, whereas *P. osorioi* is 5.50 mm long. It is similar to *P. osorioi* in the shape of the spines of tibia II on the male, but on *P. oztotl* the spiniform granules are bigger than on *P. osorioi* (Fig. 19). The cucullus is more rounded on *P. oztotl* than on *P. osorioi* (Fig. 18). The ocular areas are visible in *P. osorioi*, but in *P. oztotl* are not present (Fig. 17). The metatarsal process on *P. oztotl* is straight distally, whereas on *P. osorioi* it is hooked and shorter (Fig. 20). Metatarsus on leg III of male *P. oztotl* is rectangular, whereas on *P. osorioi* it is triangular. Tarsomere 1 of leg III on male *P. oztotl* is proportionately longer than on *P. osorioi* (Fig. 20). The basal part of tarsal process is longer on *P. oztotl* than on *P. osorioi* (Fig. 21). Finally, the tarsal process on *P. oztotl* is wider than on *P. osorioi*, and the tip is thin and straight in *P. oztotl* (Figs. 20, 21), and on *P. osorioi* it is wider and curved.

Pseudocellus oztotl is the fourth known species in which femur II is twice as long or longer than the carapace on adult males, i.e., which shows pronounced troglomorphism. In decreasing order of relative elongation (Femur II L/ Carapace L), first comes *Pseudocellus krejcae* Cokendolpher & Enriquez 2004, from Cebada Cave in Belize, with a ratio of 3.5, followed by *P. sbordoni* from Cueva de Las Canicas, Chiapas, with a ratio of 2.44, then *P. oztotl* with a ratio of 2.1, and finally *P. reddelli* from Cueva de Los Riscos, Durango, with a ratio of 2.0. Compared with *P. oztotl*, in *P. osorioi* the ratio is only 1.84; and in other cavernicolous, but slightly less troglomorphic species, the ratio is even lower, as follows: in *P. bolivari* from Grutas de Zapaluta, Chiapas 1.8; in *P. silvai* Armas 1977, from Cueva del Pirata, Cuba, it is 1.7; in *P. boneti* from Grutas de Cacahuamilpa, Guerrero, it is 1.5, as it is in *P. pearsei* from the Yucatan Peninsula.

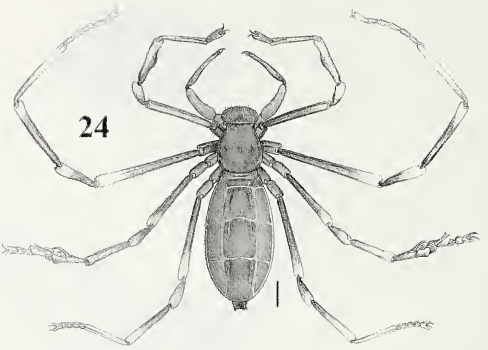


Figure 24.—*Pseudocellus platnicki* new species. Male holotype. Habitus, dorsal view. Scale = 1 mm.

Distribution.—This species is known only from the type locality (Fig. 31).

Natural history.—Cueva Las Tres Quimeras was explored by the Société Québécoise de Spéléologie in four separate expeditions from 2005 to 2009. The entrance is at 1,440 m elev.; it is 5,212 m long and drops to a depth of 815 m below entrance level. The ricinuleids were most abundant closer to the surface, where there were still big pieces of surface debris and insects floating in the water. They were found on gravel piles close to the water level (Beverly Shade, collector of the types, pers. comm., January 2011).

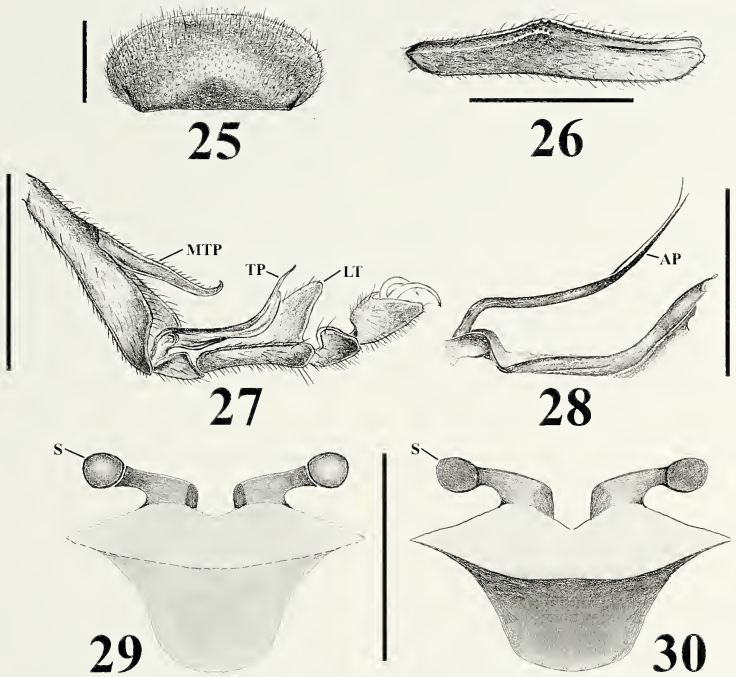
Pseudocellus platnicki new species
Figs. 24–30

Pseudocellus sp. nov. 1: Cokendolpher & Enríquez 2004:99.

Type material.—MEXICO: *Coahuila*: holotype male, Cueva Sasaparilla, Rancho Las Pilas, 130 km WSW de Ciudad Acuña (28.816667°N, 102.0000°W), 23 August 1997, D. A. Hendrickson, J. Krejca, J. C. Brown (CNAN-T0687). Paratype: 1 female (CNAN-T0688), same data as holotype.

Etymology.—This species dedicated to Dr. Norman I. Platnick (American Museum of Natural History), for his contribution to the knowledge of ricinuleids in the New World.

Diagnosis.—Males can be distinguished by a granulose prolateral hump on tibia I (Figs. 24, 26); by the long femur II (Fig. 24), 10.5 times longer than wide; by having metatarsal process long, slender and curved distally (Fig. 27); and by having the tarsal process with a sharp basal bend (Fig. 28). Females can be distinguished by the long and distally rounded spermathecae (Figs. 29, 30).



Figures 25–30.—*Pseudocellus platnicki* new species. Male holotype. 25. Cucullus, dorsal view; 26. Left tibia I, ventral view; 27. Left leg III, metatarsus and tarsal process, prolateral view; 28. Tarsal process (displaced position), prolateral view. Female paratype. Spermathecae. 29. Anterior view; 30. Posterior view. Scales = 1 mm (Figs. 26–28), 0.5 mm (Figs. 25, 29, 30).

Description.—*Male (holotype):* Carapace: Longer than wide, wider posteriorly near coxae III. Evenly pitted, with few rounded granules present along inconspicuous dorsal depression: one central, two on median part (one on each side of midline) and two on posterior part (one on each side of midline). Covered with numerous small, translucent setae (Fig. 24). Ocular areas located along coxae II and III.

Cucullus: Wider than long. Evenly pitted; with few, scattered small round granules basally (Fig. 25); covered with small translucent setae, some longer than others (Fig. 25).

Chelicerae: Fixed finger shorter than movable. Left fixed finger with six teeth, right finger with five teeth, the last two teeth longer than the others on both fingers. Left movable finger with five teeth of different sizes; right finger with five teeth, basal tooth distinctly longest.

Sternal region: Coxae I meet tritosternum in a single point; coxae II meet it along anterior third, coxae II longer than the others. All coxae evenly pitted, without granules.

Pedipalps: Coxa evenly pitted. Trochanter 1 pitted, with 1–5 granules distally. Trochanter 2, femur and tibia evenly pitted, without granules. All segments covered with translucent setae, shorter on tibia; tibia distally with a few setae longer than on other segments.

Legs: Covered with small translucent setae. All segments elongated and thin, evenly pitted, without spines and granules (Fig. 24), except granules on retrolateral part of coxa I and tibia I with a granulose prolateral hump (Figs. 24, 26). Tarsus III covered ventrally with numerous, long setae. Tarsal claws long. Tarsi I and II with a distal projection between the tarsal claws.

Copulatory apparatus: Metatarsus elongate, conical; metatarsal process elongate, curved distally (Fig. 27). Tarsomere 2 elongate, square (Fig. 27). Lamina cyathiformis of tarsomere 2 triangular (Fig. 27). Tarsal process ending in thin tip (Fig. 27).

Opisthosoma: Longer than wide, widest at midpoint along tergite XII (Fig. 24). Pitted, with few small granules anteriorly on tergites X–XII and first two marginal tergites (Fig. 24). Tergite XI wider than long, tergites XII and XIII longer than wide. Sternites evenly pitted, on sternites XI and XII quite conspicuously. Pygidium basal segment distally with small dorsal notch.

Coloration: Cucullus, carapace, pedipalps, and coxae of legs pale orange. Trochanters I and II orange, trochanters III and IV pale orange. Femorae, patellae, tibiae and metatarsi brownish, on each segment paler distally. Tarsi pale orange. Opisthosoma yellowish, sternites XI and XII dark orange. Pygidium brownish.

Figure 31.—Distribution records of *Pseudocellus chankin*, *P. jarocho*, *P. oztotl* and *P. platnicki*.

Measurements: Total length (carapace + opisthosoma + pygidium) 6.20. Carapace 1.70 long, 1.55 wide (widest part). Cucullus 0.87 long, 1.42 wide. Opisthosoma 4.30 long, 2.35 wide (widest part). Femur II l/d: 10.57. Legs tarsal formula (legs I–IV): 1-5-4-5. Leg lengths, I: coxa 0.80/ trochanter 1 0.61/ trochanter 2 -/ femur 2.30/ patella 0.82/ tibia 1.65/ metatarsus 1.77/ tarsus 0.73/ total 8.68; II: 0.90/ 0.80/ -/ 3.67/ 1.45/ 2.65/ 2.52/ 2.37/ 14.36; III: 0.81/ 0.70/ 0.81/ 2.45/ 1.07/ 1.62/ 1.25/ 1.45/ 10.16; IV: 0.73/ 0.78/ 0.76/ 2.85/ 1.05/ 1.90/ 1.75/ 1.27/ 11.09; Pedipalp: 0.7/ 0.47/ 0.32/ 1.32/ -/ 1.80/ -/ 0.30/ 4.91. Leg formula: 2431.

Female (paratype): Differs from male as follows: Tibia I without granulose prolateral hump. Cheliceral fixed finger with five teeth, distal tooth longer than the others. Both movable fingers of chelicerae with five teeth, decreasing in size distally. Cucullus, carapace and legs brown. Opisthosoma, tergites and sternites orange; sternite XI paler than the others.

Measurements: Total length 6.40. Carapace length 1.82, width 1.67 (widest part). Cucullus length 0.85, width 1.40. Opisthosoma length 4.55, width 2.50 (widest part). Femur II l/d: 10.71. Legs tarsal formula (legs I–IV): 1-5-4-5. Leg lengths, I: coxae 0.76/ trochanter 1 0.56/ trochanter 2 -/ femur 2.37/ patella 0.90/ tibia 1.75/ metatarsus 1.85/ tarsus 0.70/ total 8.89; II: 0.95/ 0.80/ -/ 3.75/ 1.50/ 2.65/ 2.55/ 2.40/ 14.60; III: 0.86/ 0.63/ 0.73/ 2.65/ 1.06/ 1.77/ 1.70/ 1.18/ 10.58; IV: 0.80/ 0.78/ 0.80/ 2.90/ 1.06/ 1.96/ 1.80/ 1.27/ 11.37; Pedipalp: 0.75/ 0.47/ 0.43/ 1.46/ -/ 1.92/ -/ 0.35/ 5.38. Leg formula: 2431.

Related species.—*P. platnicki* resembles *P. osorioi* from Cueva de Los Sabinos, San Luis Potosí, México, and *P. oztotl* from Cueva Las Tres Quimeras, Puebla, México. The resemblance with *P. osorioi* lies in the overall shape, both are large species of similar size, elongated appendages: *P. platnicki* has a total length of 6.20 mm whereas *P. osorioi* is 6.30 mm long; however, *P. platnicki* has the body and appendages evenly pitted and with very few granules, while *P. osorioi* is not pitted and has numerous granules. On *P. platnicki* the cucullus is oval (Fig. 25), whereas on *P. osorioi* it is pentagonal. Tibia I on *P. platnicki* has a granulose prolateral hump (Fig. 26), which is lacking on *P. osorioi*; tibia II on *P. osorioi* has ventral spines, whereas on *P. platnicki* it lacks spines and granules (Fig. 24). Both species resemble in the shape of the copulatory apparatus of leg III of male: *P. platnicki* has the metatarsal process thinner than *P. osorioi*; finally, *P. platnicki* has the tarsal process wider on the distal half, whereas on *P. osorioi* the tarsal process is slender and conical distally.

Pseudocellus platnicki is similar to *P. oztotl* in overall shape; also, both species have elongated appendages and similar size, *P. platnicki* is 6.20 mm long, whereas *P. oztotl* is 6.70 mm (Figs. 17, 24). Tibia I on *P. platnicki* has a granulose prolateral hump (Figs. 24, 26), while *P. oztotl* has tibia I with spines ventrally and without a granulose prolateral hump (Fig. 17); tibia II on *P. oztotl* has spines ventrally (Fig. 19), whereas on *P. platnicki* it lacks spines and granules (Fig. 24). The metatarsal process on *P. platnicki is* slender and curved distally, whereas on *P. oztotl* it is conical and straight distally (Figs. 20, 27); the tarsal process is thinner on *P. platnicki* than on *P. oztotl* (Figs. 20, 28). Finally, on females the shape of the spermathecae is very different between *P. platnicki* and *P. oztotl* (Figs. 22, 23, 29, 30).

Distribution.—This species is known only from the type locality (Fig. 31).

ACKNOWLEDGMENTS

We thank James Reddell (Texas Memorial Museum, University of Texas-Austin), James Cokendolpher (The Museum, Texas Tech University) and Peter Sprouse (Zara Environmental, Austin) for making some of the specimens available for this study. Thanks to Dr. Guillermo Ibarra Nuñez and Hector

Montaño Moreno (ECOSUR, Tapachula, Chiapas) for the loan of specimens of *Pseudocellus spinotibialis*. Special thanks to Elvia Esparza (Instituto de Biologia, UNAM) for the excellent drawings included in this work. "¡Muchas gracias a todos!" to the numerous cavers and collectors who provided specimens and/or assisted with the field work: Jesus A. Ballesteros, Diego Barrales, F. Bertoni, J. C. Brown, Andy Cobb, Jesus Cruz-Lopez, Dean Hendrickson, Jean Krejca, Jean-Francois Levis, B. Luke, Irma Mondragon, Hector Montaño-Moreno, Griselda Montiel-Parra, Guillaume Pelletier, Noe Perez, Susana Rubio, Carlos Santibañez-Lopez, and Beverly Shade (who also provided information on the cave). Thanks to the Instituto de Biología (IBUNAM), Posgrado en Ciencias Biológicas of the UNAM and Consejo Nacional de Ciencia y Tecnología (CONACYT) for their financial support. Finally, thanks to the two anonymous reviewers and the Associate Editor for improving our presentation. Specimens were collected under the Scientific Collector Permit FAUT-175 granted by SEMARNAT, Mexico, to O. F. Francke. Partial financial support was received from Bioclon, S. A. de C. V., from CONACYT, Mexico (project No. COI-043/B1 to Dra. Elena Alvarez-Buylla) and from the National Science Foundation, USA (project NSF BIO-DEB 0413453 to Dr. Lorenzo Prendini).

LITERATURE CITED

Applegate, A.D. 1999. ArcView GIS Versión 3.2. Environmental Systems Research Institute, Inc., Neuron Data, Inc., Redlands, California.

Bolivar y Pieltain, C. 1946. Hallazgo de un nuevo Ricinulideo en el México Central. Ciencia 7:24–28.

Bonaldo, A.B. & R. Pinto-da-Rocha. 2003. On a new species of *Cryptocellus* from the Brazilian Amazon (Arachnida, Ricinulei). Revista Ibérica de Aracnología 7:103–108.

Botero-Trujillo, R. & G.A. Pérez. 2008. A new species of *Cryptocellus* (Arachnida, Ricinulei) from northwestern Colombia. Journal of Arachnology 36:468–471.

Botero-Trujillo, R. & G.A. Pérez. 2009. A new species of *Cryptocellus* (Arachnida, Ricinulei) from the Kofán Territory in southwestern Colombia. Zootaxa 2050:56–64.

Cokendolpher, J.C. & T. Enríquez. 2004. A new species and records of *Pseudocellus* (Arachnida: Ricinulei: Ricinoididae) from caves in Yucatán, Mexico and Belize. Texas Memorial Museum. Speleological Monographs 6:95–99.

Cooke, J.A.L. & M.U. Shadab. 1973. New and little known ricinuleids of the genus *Cryptocellus* (Arachnida, Ricinulei). American Museum Novitates 2530:1–25.

Gertsch, W.J. 1971. Three new ricinuleids from Mexican caves (Arachnida, Ricinulei). Bulletin of the Association for Mexican Cave Studies 4:127–135.

Gertsch, W.J. & S. Mulaik. 1939. Report on a new ricinuleid from Texas. American Museum Novitates 1037:1–5.

Harvey, M.S. 2002. The neglected cousins: what do we know about the smaller arachnids orders? Journal of Arachnology 30:357–372.

Harvey, M.S. 2003. Catalogue of the Smaller Arachnid Orders of the World. CSIRO Publishing, Collinwood, Victoria, Australia.

Naskrecki, P. 2008. A new ricinuleid of the genus *Ricinoides* Ewing (Arachnida, Ricinulei) from Ghana. Zootaxa 1698:57–64.

Pinto-da-Rocha, R. & A.B. Bonaldo. 2007. A new species of *Cryptocellus* (Arachnida, Ricinulei) from Oriental Amazonia. Zootaxa 1386:47–51.

Pittard, K. & R. Mitchell. 1972. Comparative morphology of the life stages of *Cryptocellus pelaezi* (Arachnida, Ricinulei). Graduate Studies Texas Tech University. Texas Tech Press, Lubbock, Texas 1:1–77.

Platnick, N.I. & G. Pass. 1982. On a new Guatemalan *Pseudocellus* (Arachnida, Ricinulei). American Museum Novitates 2733:1–6.

Platnick, N.I. & L.F. García. 2008. Taxonomic notes on Colombian *Cryptocellus* (Arachnida, Ricinulei). Journal of Arachnology 36:145–149.

Selden, P.A. 1992. Revision of the fossil ricinuleids. Transactions of the Royal Society of Edinburgh: Earth Sciences 83:595–634.

Teruel, R. & L.F. Armas. 2008. Nuevo *Pseudocellus* Platnick 1980 de Cuba oriental y nuevos registros de *Pseudocellus paradoxus* (Cooke 1972) (Ricinulei: Ricinoididae). Boletín de la Sociedad Entomológica Aragonesa 43:29–33.

Tourinho, A.L. & C.S. Azevedo. 2007. A new Amazonian *Cryptocellus* Westwood (Arachnida, Ricinulei). Zootaxa 1540:55–60.

Tourinho, A.L., N.F. Lo Man-Hung & A.B. Bonaldo. 2010. A new species of Ricinulei of the genus *Cryptocellus* Westwood (Arachnida) from northern Brazil. Zootaxa 2684:63–68.

Tourinho, A.L. & R. Saturnino. 2010. On the *Cryptocellus peckorum* and *Cryptocellus adisi* groups, and description of a new species of *Cryptocellus* from Brazil (Arachnida: Ricinulei). Journal of Arachnology 38:425–432.

Manuscript received 23 January 2011, revised 8 April 2011.

Appendix 1.—Material examined to make the key for identification of Mexican *Pseudocellus:*

Pseudocellus boneti: México: Guerrero: 1 ♂ (CNAN-Ri0009) from Gruta de Acuitlapan (cave); 1 ♀ (CNAN-Ri0010), same location; 1 ♂ (CNAN-Ri0011) from Gruta de la Mariposa, Tetipac (cave); 1 ♀ (CNAN-Ri0012), same location.

Pseudocellus gertschi: México: Veracruz: 3♀, 3 nymphs (CNAN-Ri0002) from Estación Biológica de la UNAM "Los Tuxtlas" (litter).

Pseudocellus osorioi: México: San Luis Potosi: 3 ♀, 1 nymph (CNAN-Ri0004) from Sótano del Tigre, Sierra del Abra (cave); Tamaulipas: 1 ♀ (CNAN-Ri0008) from Cueva de Quintero (cave).

Pseudocellus pearsei: México: Quintana Roo: 1 ♂ (CNAN-Ri0013) from Caverna "Aktum Chen" (cave); Yucatán: 2 ♂, 4 ♀, 12 nymphs (CNAN-Ri0007) from Cenote Mayapan (cave); 3 ♂, 2 ♀, 2 nymphs (CNAN-Ri0014) from Acutun Isban, 1.3 km SE of San Francisco Grande (litter); 1 ♂, 2 ♀, 1 nymph (CNAN-Ri0015), same location; 4 ♀ (CNAN-Ri0016) from Cenote Xcoptiel, Xcoptiel, 4.5 km SSW Dzeal. (cave); 6 ♂, 3 ♀, 3 nymphs (CNAN-Ri0017) from Actun Olem, 1.4 km N Xbohom (litter); 2 ♂, 3 ♀, 1 nymph (CNAN-Ri0018) from Actun Yax, 5.2 km SSW Kaua (cave); 4 ♀, 2 nymphs (CNAN-Ri0019) from Grutas de San Daniel, 1.6 km N of Quintana Roo Plaza (cave).

Pseudocellus pelaezi: México: Tamaulipas: 2 ♂, 2 ♀, 4 nymphs (CNAN-Ri0005) from Cueva de la Florida, Sierra del Abra (cave).

Pseudocellus spinotibialis: México: Chiapas: 1 ♂ (ECOTAAR-Ri00001), 1 ♂ (ECOTAAR-Ri00002), 1 ♀ (ECOTAAR-Ri00003), 1 ♀ (ECOTAAR-Ri00007), 1 ♀ (ECOTAAR-Ri00009) from Unión Juárez, Talquian C. (cave).

2011. The Journal of Arachnology 39:378–383

Evidence that olfaction-based affinity for particular plant species is a special characteristic of *Evarcha culicivora*, a mosquito-specialist jumping spider

Ximena J. Nelson[1] and **Robert R. Jackson**[1,2]: [1]School of Biological Sciences, University of Canterbury, Private Bag 4800, Christchurch, New Zealand. E-mail: ximena.nelson@canterbury.ac.nz; [2]International Centre of Insect Physiology and Ecology, Thomas Odhiambo Campus, P.O. Box 30 Mbita Point, Kenya

Abstract. *Evarcha culicivora*, an East African jumping spider (family Salticidae), was shown in an earlier study to have an affinity for the odor from two particular plant species, *Lantana camara* and *Ricinus communis*. The olfactometer used in the earlier study was designed for choice testing. Here we focus on *L. camara* and, by using a second olfactometer method (retention testing), add to the evidence that the odor of this plant is salient to *E. culicivora*. Another 17 East African salticid species, all from different genera, were investigated using the same two olfactometer designs as used when investigating *E. culicivora*. The number of individuals of each of these 17 species that chose *L. camara* odor was not significantly different from the number that chose a no-odor control and, for each species, the latency to leave a holding chamber (retention time) in the presence of *L. camara* odor was not significantly different from retention time in the presence of a no-odor control. Based on these findings, we conclude that, rather than being a widespread salticid characteristic, an affinity for the odor of *L. camara* is a special characteristic of *E. culicivora*.

Keywords: Plant-arthropod interactions, *Lantana camara*, Salticidae, olfaction

Many insects that specialize at feeding on nectar and pollen associate with particular plant species (e.g., Chittka et al. 1999; Waser & Ollerton 2006; Díaz et al. 2007), and many insects are known to rely on specific blends of plant-derived volatile compounds for identifying the particular plant species they exploit as sites for feeding or oviposition (e.g., Pichersky & Gershenzon 2002; Bruce et al. 2005; Anfora et al. 2009; Karlsson et al. 2009). There are also examples of spiders that associate with particular types of plants, especially pitcher plants (Cresswell 1993) and bromeliads (Romero & Vasconcellos-Neto 2004, 2005). Besides offering opportunity for nectar and pollen meals (Vogelei & Greissl 1989; Pollard et al. 1995; Jackson et al. 2001; Taylor & Pfannenstiel 2008, 2009; Taylor & Bradley 2009), associating with plants may reward spiders with opportunity to feed on other plant products (Meehan et al. 2009) and on insects that land on the plants (Ruhren & Handel 1999; Whitney 2004). In some instances, the benefits of associating with plants may include opportunity to feed on insects ensnared by the plant's sticky glandular hairs (Vasconcellos-Neto et al. 2007).

Little is known about the chemical cues by which spiders might identify specific plant species, but spiders are known to make use of chemosensory information regarding the sex, maturity, virgin-mated status, and fighting ability of conspecific individuals (Pollard et al. 1987; Clark et al. 1999; Roberts & Uetz 2005). Chemical cues are also known to be used by some spiders for detecting prey (Blanke 1972; Persons & Rypstra 2000; Clark et al. 2000a,b; Jackson et al. 2002, 2005) and predators (Persons et al. 2002; Li & Lee 2004; Li & Jackson 2005), and for determining the individual attractiveness of potential mates (Searcy et al. 1999; Roberts & Uetz 2005; Cross et al. 2009).

Two studies in particular suggest that further research is needed on how spiders might make use of plant-derived volatile compounds when identifying particular plant species. One of these studies showed associative learning by 'ghost spiders' (*Hibana futilis* Banks 1898, Anyphaenidae) when artificial odor was paired with artificial nectar (Patt & Pfannenstiel 2008). The other study showed that *Evarcha culicivora*, an East African salticid, responds in olfactometer experiments to the odor of two particular plant species on which it is commonly found, *Lantana camara* and *Ricinus communis* (Cross & Jackson 2009). That these two plant species might have a role in the mating system of *E. culicivora* has been suggested by other research (Cross et al. 2008) in which it was shown that, when on these plants, the courtship behavior of *E. culicivora* is more variable in display sequencing, more active, and more persistent. These effects are not evident during intraspecific interactions on a variety of other plant species (RRJ unpubl. data).

Here we focus on *L. camara* in particular and test 17 additional East African salticids with the odor of this plant species. Our hypothesis is that an affinity for the odor of *L. camara* is a special characteristic of *E. culicivora*. The rationale for testing other salticids is to consider, as an alternative hypothesis, the possibility that having an affinity for *L. camara* odor is a widespread salticid characteristic. Besides using choice-test olfactometers with these 17 salticid species (as adopted in Cross & Jackson's (2009) study on *E. culicivora*), we also use retention-test olfactometers in experiments with these 17 salticids and with *E. culicivora*. Retention-test olfactometers are used for determining how long a test spider will remain in a small holding chamber when exposed to specific odors. This type of testing has been used in earlier research with *E. culicivora* (Cross et al. 2009), but never before specifically for examining response to plant odor.

METHODS

General.—Olfactometer testing was carried out using salticids from laboratory cultures (F2 and F3 generation). Rearing methods, as well as the basic procedures used in olfactometer experiments, were as in earlier research (Cross & Jackson 2009; Cross et al. 2009) and only essential details are provided here.

For rearing and maintenance, each spider was fed to satiation three times a week on blood-carrying female mosquitoes (*Anopheles gambiae s.s.* from laboratory culture) and 'lake flies' (*Nilodorum brevibucca*, Chironomidae; collected as needed from field). Hunger level was standardized by subjecting each test spider to a 7-day pre-trial fast.

Two olfactometer methods were used (choice testing and retention testing), with the odor source being a plant cutting held in an odor chamber (glass-cube box). Each cutting was two *Lantana camara* umbels (clusters of flowers) with accompanying leaves and stems (no flowers senescent) taken from the field immediately before setting up for an experiment; median weight/umbel (1st and 3rd quartiles) = 364 (329 and 384) mg, (n=10). Disposable surgical gloves were worn while collecting and handling plant material.

Testing was carried out between 0800 h and 1400 h (laboratory photoperiod 12L:12D, lights on at 0700 h). Between trials, olfactometers were dismantled and cleaned with 80% ethanol followed by distilled water and then dried in an oven. Airflow in the olfactometers was adjusted to 1500 ml/min (Matheson FM-1000 airflow regulator) and there was no evidence that this setting had any adverse effects on the salticid's locomotion or other behavior. The spiders used in choice tests were different from the spiders used in retention tests, but no test spiders had prior experience with plants. No spider was used in more than one choice test or more than one pair (experimental one day, control another day) of retention tests. All test spiders were adults that matured 2–3 wk before being tested and none had mated. Both sexes of all speeies were used in choice testing, but only males were used in retention testing.

Choice testing.—Y-shaped glass olfactometers were used for choice testing (Fig. 1a). The two ends of the Y were the 'choice arms', with each choice arm being connected to an odor chamber. Which of the two odor chambers contained the plant cutting was determined at random. Air was pumped separately into the two odor chambers and then through the choice arms before converging at the stem of the Y ('test arm').

Before testing began, the test spider (n = 70 per sex and species) was confined for 2 min in a holding chamber at the far end of the test arm. While in the holding chamber, the test spider's access to the test arm was blocked by a removable metal grill that fit within a slit in the chamber roof. Testing began by lifting the grill. When the spider entered a choice arm and remained there for 30 s, we recorded the arm entered as the test spider's choice. The spider was allowed 30 min within which to make a choice and the number of spiders that failed to make a choice was, for each species, always fewer than 5% of the spiders tested.

Retention testing.—During retention testing, air was pushed successively through an odor chamber, a holding chamber and an exit chamber (Fig. 1b). The holding chamber was a glass tube (rubber stopper in one end, other end open). The open end of the holding chamber fit securely in the hole in the glass cube that formed the exit chamber, flush with the inner wall of the exit chamber. At the other end of the holding chamber, there was a hole in the stopper with a glass tube going through to the odor chamber, which was identical in size to the exit chamber (see Fig. 1b for dimensions). A nylon-netting screen over the stopper (new netting for each test) ensured that the test spider could not enter the odor chamber, the only way out of the holding chamber being via the opening into the exit chamber. The exit chamber was another glass cube identical to the odor chamber.

The test spider (n = 20 for each species) was first kept in the holding chamber for 2 min, with the holding chamber not yet connected to the stimulus and exit chambers. The end of the holding chamber that would go into the exit chamber was plugged with a rubber stopper. To begin a test, this stopper was removed and the holding chamber was positioned between the stimulus and exit chamber, but with a prerequisite being that the test spider had to be in the half of the holding chamber distal to the exit chamber. If this prerequisite was not met at the end of the 2-min pre-test period, the beginning of the test was delayed until the spider moved on its own accord into the distal half of the chamber and remained there for 2 min. Testing was aborted if this criterion was still not met after waiting 15 min, but aborted tests were rare (< 5% for any given species).

No-odor control tests and odor tests were randomized. Once testing began, we recorded retention time (i.e., the test spider's latency to leave the holding chamber, defined as the time elapsing between the beginning of a test and departure by the spider into the exit chamber; maximum time allowed, 60 min). By default, the spider's retention time was recorded as 60 min whenever the 60-min test period ended with the test spider still in the holding chamber.

Data analysis.—Choice-test data were analyzed using tests for goodness of fit (H_o = 50:50) and retention-testing data were analyzed using non-parametric Wilcoxon tests for paired comparisons (null hypothesis: latency to leave holding chamber when tested with odor source matched latency to leave holding chamber when tested with no-odor control). Retention testing data are shown based on each test spiders' calculated absolute difference score (subtracting its latency to leave holding chamber when tested with control from latency to leave holding chamber when tested with odor), resulting in positive scores when the spider spent more time in the holding chamber when tested with odor, and resulting in negative scores when spider spent more time in the holding chamber when tested with no odor.

Voucher specimens of all species have been deposited in the Florida State Collection of Arthropods, Gainesville, Florida, USA.

RESULTS

Choice-test data from males and females of each speeies did not differ in any case, so these data were pooled for simplification. In the earlier study (Cross & Jackson 2009), *Evarcha culicivora* chose *Lantana camara* odor signifieantly more often than the no-odor control in choice-test olfactometers (Fig. 2) and, in the present study, *E. culicivora* had a significantly longer latency to leave the holding chamber when in the presence of *L. camara* odor than when in the presence of a no-odor control. However, for the other 17 salticid species, the number of individuals that chose *L. camara* odor was not significantly different from the number that chose the no-odor control in the choice-test olfactometers. In the retention-test olfactometers the retention time in the presence of *L. camara* odor was also not significantly different, for these 17 species,

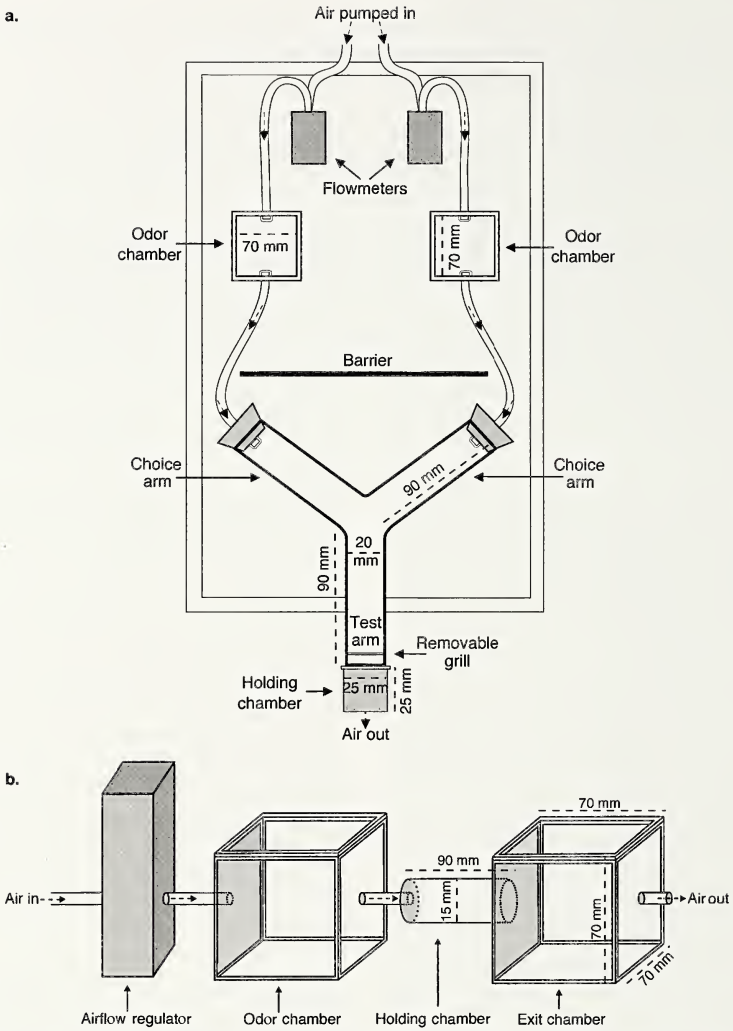


Figure 1.—Olfactometers used for: **a.** choice testing (view of odor source obstructed by opaque barrier) and **b.** retention testing (view of odor source obstructed by black paper taped to outside of odor chamber wall that faced holding chamber). Dashed arrows indicate direction of airflow. Not drawn to scale.

from retention time in the presence of the no-odor control (Table 1, Fig. 3; note non-significant trend for *Natta rufopicta* to display greater retention in the control tests). In concordance with results from olfactometer choice tests, *L. camara* odor did induce a significant retention in *E. culicivora* (Table 1).

DISCUSSION

The earlier study (Cross & Jackson 2009) demonstrated that the odor of *Lantana camara* is salient to *Evarcha culicivora*, but left unresolved the question of whether responsiveness to *L. camara* odor by *E. culicivora* is an unusual characteristic of this particular salticid species or, alternatively, a characteristic

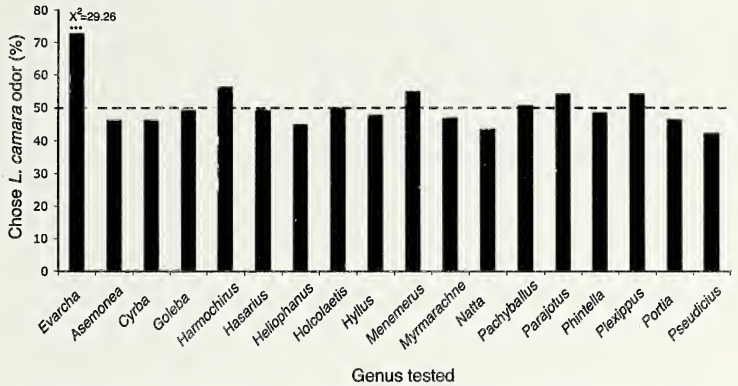


Figure 2.—Pooled results from olfactometer choice-tests. *Evarcha culicivora* chose odor arm significantly more often control arm (data from Cross and Jackson 2009). For all other salticid species, number of individuals that chose odor not significantly different from number that chose control. Dashed line denotes 50%. n = 140. χ^2 = test of goodness of fit. *** $P < 0.0001$.

that is widespread in the Salticidae. Here we investigated another 17 salticid species, all from different genera, from East Africa. For each of these species, when we used the same odor-based choice-testing methods and achieved the same sample sizes as in the earlier experiments with *E. culicivora*, the number of individuals that chose *L. camara* odor was not significantly different from the number that chose the no-odor control. Using the retention-testing olfactometers, we again found evidence that the odor of *L. camara* is salient to *E. culicivora* and, for retention tests, as for choice tests, the response to *L. camara* odor by each species other than *E. culicivora* was not significantly different from response to no-odor controls.

Table 1.—Test results for Wilcoxon-tests comparing latency to leave holding chamber in control or experimental tests. The difference in time beween these is depicted in Fig. 3. All spiders sourced in Kenya except *Parajotus cinereus* (from Uganda).

Test spider species	*W*	*P*
Evarcha culicivora Wesolowska & Jackson 2003	176.0	0.0004
Asemonea murphyae Wanless 1980	−26.0	0.61
Cyrba ocellata (Kroneberg 1875)	70.0	0.16
Goleba puella (Simon 1885)	−31.0	0.58
Harmochirus brachiatus (Thorell 1877)	65.0	0.20
Hasarius adansoni (Savigny et Audouin 1825)	3.0	0.97
Heliophanus sp.	51.0	0.24
Holcolaetis vellerea (Simon 1909)	−21.0	0.69
Hyllus sp.	50.0	0.29
Menemerus congoensis Lessert 1925	28.0	0.56
Myrmarachne melanotarsa Wesolowska & Salm 2002	73.0	0.15
Natta rufopicta (Simon 1909)	82.0	0.08
Pachyballus cordiformis Berland et Millot 1941	13.0	0.78
Parajotus cinereus Wesolowska 2004	19.0	0.70
Phintella sp.	−1.0	1.00
Plexippus sp.	60.0	0.27
Portia africana (Simon 1885)	9.0	0.85
Pseudicius sp.	40.0	0.43

As there are more than 5,000 described species in the family Salticidae (Platnick 2010), our findings should not be construed as proving that *E. culicivora* is absolutely unique, but it seems unlikely that responsiveness to *L. camara* odor is widespread within the Salticidae.

The precise role of *L. camara* in the biology of *E. culicivora* is poorly understood. Earlier research (Cross et al. 2008) suggested that we need a better understanding of the role plants might play in the mating strategy of *E. culicivora*, but plants may also have a role in its feeding strategy. As *E. culicivora* is known to feed on nectar (RRJ unpubl. data), one hypothesis that should be considered is that responding to *L. camara* odor is related to visiting this plant species for nectar meals. This would make *E. culicivora* comparable to *Heliconius melpomene*, a butterfly that, by responding to the odor of *L. camara*, locates and feeds on the nectar of this plant (Andersson et al. 2002; Andersson & Dobson 2003). However, there is a complication with any hypothesis concerning *E. culicivora* having evolved mechanisms of exploiting specifically *L. camara*. This plant species is native to the Americas and is an introduced weed in many parts of the world, including East Africa (Day et al. 2003). We need a better understanding of how *E. culicivora* responds to a wider range of plant species, including native species with which it has shared a longer evolutionary history, in addition to the primary volatile components of various plants, before we can tease apart the basis of this affinity. This large topic is the subject of ongoing research.

Evarcha culicivora has an unusual predatory strategy, as its preferred prey are blood-carrying mosquitoes (Jackson et al. 2005). An alternative hypothesis is that this mosquito-specialist spider locates its prey by visiting *L. camara* or other plants. Only female mosquitoes feed on blood (Clements 1999). Male mosquitoes feed primarily on nectar, but *E. culicivora* is proficient at discriminating between males and

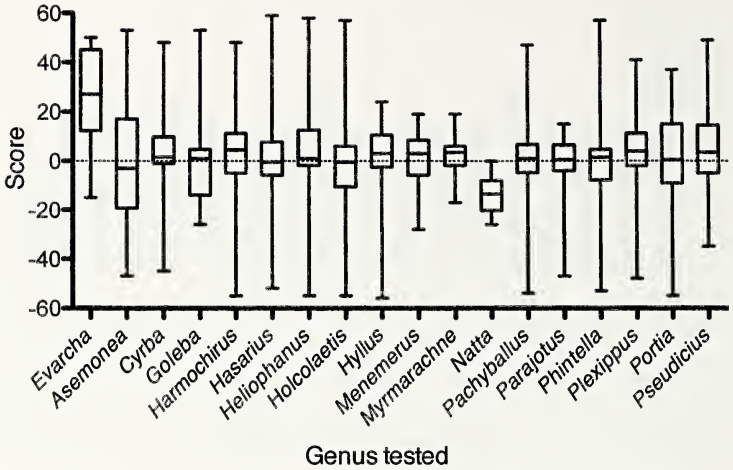


Figure 3.—Boxplots (median and quartiles) with whiskers (min and max) for retention testing for all species. Score calculated by subtracting latency to leave holding chamber when tested with control from latency to leave holding chamber when tested with odor (positive score: spider spent more time in the holding chamber when tested with odor; negative score: spider spent more time in the holding chamber when tested with control). $n = 20$.

females, has an active preference for female mosquitoes as prey and chooses *Anopheles* in preference to other mosquitoes (Nelson & Jackson 2006). However, it is now well established that visiting plants for nectar meals is important not only for the male but also for the female of a variety of mosquito species, including *Anopheles* species (McCrae et al. 1969, 1976; Gujral & Vasudevan 1983; Clements 1999; Foster & Takken 2004; Impoinvil et al. 2004; Manda et al. 2007a,b). However, it is unlikely that encounters between *E. culicivora* and female mosquitoes, including *Anopheles*, often happen on *L. camara* or other plants, as *E. culicivora*, like most salticids (Richman & Jackson 1992), appears to be active as a predator during daylight hours (RRJ unpubl. data) while its prey, the female mosquito, probably feeds from plants primarily at night. This problem notwithstanding, *E. culicivora* might find mosquitoes during the daytime resting post-feeding in the vicinity of the plants to which the spider and the mosquito have been attracted, albeit at different times.

ACKNOWLEDGMENTS

We thank Godfrey Otieno Sune, Stephen Abok Aluoch and Jane Atieno Obonyo for their assistance at ICIPE. We also gratefully acknowledge support from the Royal Society of New Zealand (Marsden Fund (M1096, M1079) and James Cook Fellowship (E5097)), the National Geographic Society (8676-09, 6705-00), and the US National Institutes of Health (R01-AI077722).

REFERENCES

Andersson, S. & H.E.M. Dobson. 2003. Behavioral foraging responses by the butterfly *Heliconius melpomene* to *Lantana camara* floral scent. Journal of Chemical Ecology 29:2303–2318.

Andersson, S., L.A. Nilsson, I. Groth & G. Bergström. 2002. Floral scents in butterfly-pollinated plants: possible convergence in chemical composition. Botanical Journal of the Linnean Society 140:129–153.

Anfora, G., M. Tasin, A. De Crostofaro, C. Ioriatti & A. Lucchi. 2009. Synthetic grape volatiles attract mated *Lobesia botrana* females in laboratory and field bioassays. Journal of Chemical Ecology 35:1054–1062.

Blanke, R. 1972. Untersuchungen zur Ökophysiologie und Ökethologie von *Cyrtophora citricola* Forskål (Araneae, Araneidae) in Andalusien. Forma et Functio 5:125–206.

Bruce, T.J.A., L.J. Wadhams & C.M. Woodcock. 2005. Insect host location: a volatile situation. Trends in Plant Science 10:269–274.

Chittka, L., J.D. Thomson & N.M. Waser. 1999. Flower constancy, insect psychology, and plant evolution. Naturwissenschaften 86: 361–377.

Clark, R.J., R.R. Jackson & J.R. Waas. 1999. Draglines and assessment of fighting ability in cannibalistic jumping spiders. Journal of Insect Behavior 12:753–766.

Clark, R.J., D.P. Harland & R.R. Jackson. 2000a. Speculative hunting by an araneophagic salticid spider. Behaviour 137: 1601–1612.

Clark, R.J., R.R. Jackson & B. Cutler. 2000b. Chemical cues from ants influence predatory behavior in *Habrocestum pulex* (Hentz), an ant-eating jumping spider (Araneae, Salticidae). Journal of Arachnology 28:299–341.

Clements, A.N. 1999. The Biology of Mosquitoes. CABI Publishing, Wallingford, UK.

Cresswell, J.E. 1993. The morphological correlates of prey capture and resource parasitism in pitchers of the carnivorous plant *Sarracenia purpurea*. American Midland Naturalist 129:35–41.

Cross, F.R., R.R. Jackson & S.D. Pollard. 2008. Complex display behaviour of *Evarcha culicivora*, an East African mosquito-eating jumping spider. New Zealand Journal of Zoology 35:151–187.

Cross, F.R. & R.R. Jackson. 2009. Odour-mediated response to plants by *Evarcha culicivora*, a blood-feeding jumping spider from East Africa. New Zealand Journal of Zoology 36:75–80.

Cross, F.R., R.R. Jackson & S.D. Pollard. 2009. How blood-derived odor influences mate-choice decisions by a mosquito-eating

predator. Proceedings of the National Academy of Science USA 46:19416–19419.

Day, M.D., C.J. Wiley, J. Playford & M.P. Zalucki. 2003. *Lantana*: Current Management Status and Future Prospects. CABI Publishing, Canberra.

Díaz, P.C., C. Gruter & W.M. Farina. 2007. Floral scents affect the distribution of hive bees around dancers. Behavioral Ecology & Sociobiology 61:1589–1597.

Foster, W.A. & W. Takken. 2004. Nectar-related vs. human-related volatiles: behavioural response and choice by female and male *Anopheles gambiæ* (Diptera : Culicidae) between emergence and first feeding. Bulletin of Entomological Research 94:145–157.

Gujral, G.S. & P. Vasudevan. 1983. *Lantana camara* L., a problem weed. Journal of Scientific and Industrial Research 42:281–286.

Impoinvil, D.E., J.O. Kongere, W.A. Foster, B.N. Njiru, G.F. Killeen, J.I. Githure, J.C. Beier, A. Hassanali & B.G.J. Knols. 2004. Feeding and survival of the malaria vector *Anopheles gambiæ* on plants growing in Kenya. Medical and Veterinary Entomology 18:1–8.

Jackson, R.R., R.J. Clark & D.P. Harland. 2002. Behavioural and cognitive influences of kairomones on an araneophagic spider. Behaviour 139:749–775.

Jackson, R.R., X.J. Nelson & G.O. Sune. 2005. A spider that feeds indirectly on vertebrate blood by choosing female mosquitoes as prey. Proceedings of the National Academy of Science USA 102:15155–15160.

Jackson, R.R., S.D. Pollard, X.J. Nelson, G.B. Edwards & A.T. Barrion. 2001. Jumping spiders (Araneae: Salticidae) that feed on nectar. Journal of Zoology 255:25–29.

Karlsson, M.F., G. Birgersson, A.M.C. Prado, F. Bosa, M. Bengtsson & P. Witzgall. 2009. Plant odour analysis of potato response of Guatemalan moth to above- and belowground potato volatiles. Journal of Agricultural and Food Chemistry 57:5903–5909.

Li, D. & R.R. Jackson. 2005. Influence of diet-related chemical cues from predators on the hatching of egg-carrying spiders. Journal of Chemical Ecology 31:333–342.

Li, D. & W.S. Lee. 2004. Predator-induced plasticity in web-building behaviour. Animal Behaviour 67:309–318.

Manda, H., L.C. Gouagna, W.A. Foster, R.R. Jackson, J.C. Beier, J.I. Githure & A. Hassanali. 2007a. Effect of discriminative feeding from different plant species on the survival and fecundity of *Anopheles gambiæ* s.s. Malaria Journal 6:e113.

Manda, H., L.C. Gouagna, E. Nyandat, E.W. Kabiru, R.R. Jackson, W.A. Foster, J.I. Githure, J.C. Beier & A. Hassanali. 2007b. Discriminative feeding behaviour of *Anopheles gambiæ* s.s. on endemic plants in western Kenya. Medical and Veterinary Entomology 21:103–111.

McCrae, A.W.R., Y. Ssenkubuge, P. Manuma, C. Mawjje & A. Kitama. 1969. Mosquito and tabanid activity at plant sugar sources. Repository of the East African Virus Research Institute 18:96–102.

McCrae, A.W.R., P.F.L. Boreham & Y. Ssenkubuge. 1976. The behavioural ecology of host selection in *Anopheles implexus* (Theobald) (Diptera, Culicidae). Bulletin of Entomological Research 66:587–631.

Meehan, C.J., E.J. Olson, M.W. Reudink, T.K. Kyser & R.L. Curry. 2009. Herbivory in a spider through exploitation of an ant-plant mutualism. Current Biology 19:R882–R883.

Nelson, X.J. & R.R. Jackson. 2006. A predator from East Africa that chooses malaria vectors as preferred prey. PLoS ONE 1(1):e132. Doi:10.1371/journal.pone.0000132.

Patt, J.M. & R.S. Pfannenstiel. 2008. Odor-based recognition of nectar in cursorial spiders. Entomologia Experimentalis et Applicata 127:64–71.

Persons, M.H. & A.L. Rypstra. 2000. Preference for chemical cues associated with recent prey in the wolf spider *Hogna helluo* (Araneae: Lycosidae). Ethology 106:27–35.

Persons, M.H., S.E. Walker & A.L. Rypstra. 2002. Fitness costs and benefits of antipredator behavior mediated by chemotactile cues in the wolf spider *Pardosa milvina* (Araneae: Lycosidae). Behavioral Ecology 13:386–392.

Pichersky, E. & J. Gershenzon. 2002. The formation and function of plant volatiles: perfumes for pollinator attraction and defense. Current Opinion in Plant Biology 5:237–243.

Plantick, N.I. 2010. World Spider Catalogue, Version 11.0 American Museum of Natural History, New York. Online at http://research.amnh.org/iz/spiders/catalog/COUNTS.html

Pollard, S.D., A.M. MacNab & R.R. Jackson. 1987. Communication with chemicals: pheromones and spiders. Pp. 133–141. *In* Ecophysiology of Spiders. (W. Nentwig, ed.). Springer-Verlag, Berlin.

Pollard, S.D., M.W. Beck & G.N. Dodson. 1995. Why do male crab spiders drink nectar. Animal Behaviour 49:1443–1448.

Richman, D.B. & R.R. Jackson. 1992. A review of the ethology of jumping spiders (Araneae, Salticidae). Bulletin of the British Arachnological Society 9:33–37.

Roberts, J.A. & G.W. Uetz. 2005. Information content of female chemical signals in the wolf spider, *Schizocosa ocreata*: male discrimination of reproductive state and receptivity. Animal Behaviour 70:217–223.

Romero, G.Q. & J. Vasconcellos-Neto. 2004. Beneficial effects of flower-dwelling predators on their host plant. Ecology 85:446–457.

Romero, G.Q. & J. Vasconcellos-Neto. 2005. The effects of plant structure on the spatial and microspatial distribution of a bromeliad-living jumping spider (Salticidae). Journal of Animal Ecology 74:12–21.

Ruhren, S. & S.N. Handel. 1999. Jumping spiders (Salticidae) enhance the seed production of a plant with extrafloral nectaries. Oecologia 119:227–230.

Searcy, L.E., A.L. Rypstra & M.H. Persons. 1999. Airborne chemical communication in the wolf spider *Pardosa milvina*. Journal of Chemical Ecology 25:2527–2533.

Taylor, R.M. & R.A. Bradley. 2009. Plant nectar increases survival, molting, and foraging in two foliage wandering spiders. Journal of Arachnology 37:232–237.

Taylor, R.M. & R.S. Pfannenstiel. 2008. Nectar feeding by wandering spiders on cotton plants. Environmental Entomology 37:996–1002.

Taylor, R.M. & R.S. Pfannenstiel. 2009. How dietary plant nectar affects the survival, growth, and fecundity of a cursorial spider *Cheiracanthium inclusum* (Araneae: Miturgidae). Environmental Entomology 38:1379–1386.

Vasconcellos-Neto, J., G.Q. Romero, A.J. Santos & A.S. Dippenaar-Schoeman. 2007. Associations of spiders of the genus *Peucetia* (Oxyopidae) with plants bearing glandular hairs. Biotropica 39:221–226.

Vogelei, A. & R. Greissl. 1989. Survival strategies of the crab spider *Thomisus onustus* Walckenaer 1806 (Chelicerata, Arachnida, Thomisidae). Oecologia 80:513–515.

Waser, N.M. & J. Ollerton. 2006. Plant-Pollinator Interactions: from Specialization to Generalization. University of Chicago Press, Chicago, Illinois.

Whitney, K.D. 2004. Experimental evidence that both parties benefit in a facultative plant-spider mutualism. Ecology 85:1642–1650.

Manuscript received 7 April 2011, revised 24 May 2011.

2011. The Journal of Arachnology 39:384–392

Eresus kollari (Araneae: Eresidae) calls for heathland management

Rolf Harald Krause[1], **Jörn Buse**[2], **Andrea Matern**[1], **Boris Schröder**[3,4], **Werner Härdtle**[1] and **Thorsten Assmann**[1]: [1]Institute of Ecology, Leuphana University Lüneburg, Scharnhorststrasse 1, 21335 Lüneburg, Germany. E-mail: Krause@uni.leuphana.de; [2]Institute of Zoology, Department of Ecology, Johannes Gutenberg-University Mainz, Johann-Joachim-Becherweg 13, 55099 Mainz, Germany; [3]Institute of Earth and Environmental Science, University of Potsdam, Karl-Liebknecht-Strasse 24-25, 14476 Potsdam, Germany; [4]Leibniz-Centre for Agricultural Landscape Research (ZALF), Eberswalder Strasse 84, 15374 Müncheberg, Germany

Abstract. Northwest Europe's largest heather-dominated sandy habitats are located in the nature reserve Lüneburger Heide, Germany. Yet, even these appear to be losing their ability to support some of their stenotopic species such as the ladybird spider, *Eresus kollari* Rossi 1846, and are thus becoming increasingly important for the preservation of these species. The habitat requirements of this endangered spider species were investigated in order to obtain data that will help stabilize the last remnants of the species' population in northwest Germany. Several heathland habitats were surveyed by pitfall trapping during the mate-search period of the males. Two statistical methods were applied: logistic regression and boosted regression trees (BRT). Both methods showed that three habitat variables are of prime relevance in predicting the occurrence of *E. kollari*: a) thickness of the organic layer (a negative effect), b) soil temperature at a depth of 10 cm, and c) *Calluna* cover in the herb layer (both have positive effect). Our results show that choppering (removing above-ground biomass and most of O-layer) and burning are likely appropriate heathland management measures for the conservation of *E. kollari*. Such measures improve the species' habitat quality by creating a heterogenic (small-scaled) heathland structure with suitable microhabitats. As *Calluna* heathlands show a clear senescence of the dominant heather, it is essential that those habitat patches be conserved. Further measures, such as transfer experiments, are recommended.

Keywords: Conservation management, habitat modeling, action plan, choppering, burning

The decline of European heathland, semi-natural habitats dominated by the heather species *Calluna vulgaris*, over the last two centuries due to changes in agricultural use and forestation (Webb 1998) has resulted in serious threats for the given habitat types, especially due to fragmentation and reduced habitat quality. Heathlands have thus been designated one of the most endangered habitat types on a European and regional scale (The Council of the European Communities 2004; Webb 1998; Keienburg et al. 2004).

Sandy heathlands do not provide a homogeneous habitat in time and space, because they are largely influenced by the developmental cycle of the dominant plant species *Calluna vulgaris* (Gimingham 1972). The largest remnants of heather-dominated sandy habitats in northwest Europe have been preserved in the Lüneburger Heide and are now part of a large nature reserve. Between 1850 and 1960, the proportion of heathland declined from 77% to 21% and today represents less than 5% of the nature reserve (Völksen 1993; Assmann 1999; Keienburg & Prüter 2004). These heathland remnants have enabled the survival of a stenotopic invertebrate fauna. However, a striking decrease in the numbers of certain stenotopic arthropod species has been observed, whereas other stenotopic heathland species still seem to be widespread (Desender et al. 1994; Assmann et al. 2003; Maes & Van Dyck 2005) or relatively stable (Gajdoš & Toft 2000).

Effective conservation of the heathland-specific arthropod species that are declining in the Lüneburger Heide can only be successful if their habitat requirements are understood and appropriate heathland management measures are implemented (Assmann & Janssen 1999). This requires detailed knowledge of the specific microhabitat in which they occur.

Assessment of distribution modeling is an important approach to obtain scientific evidence regarding the habitat preferences of selected species. Several recent studies have demonstrated the use of such models to obtain predictors for the occurrence of endangered arthropod species, including potential conservation activities (Binzenhöfer et al. 2005, 2008; Buse et al. 2007; Hein et al. 2007; Matern et al. 2007; Heisswolf et al. 2009).

Here, we report the habitat requirements of the ladybird spider *E. kollari* Rossi 1846 as an example of a stenotopic heathland species declining in number. The males' conspicuousness has made this spider a well-known species, not only among zoologists. Although its taxonomy and systematics have only recently been clarified by Řezáč et al. (2008), the decrease in numbers of *E. kollari* is well documented (Johannesen & Veith 2001). It is placed on red lists throughout Germany (Platen et al. 1996; Finch 2004).

Eresus kollari and its sibling species *E. sandaliatus* are both well known across northern Europe. A large-scale governmental conservation project in England involving a comprehensive action plan for *E. sandaliatus* over nearly two decades has proved successful (Hughes et al. 2009).

The aim of our research was to 1) determine the specific habitat requirements of *E. kollari* and 2) suggest specific habitat management measures aimed at conserving the last populations of the ladybird spider in northwest Germany. Bell et al. (2001) states that management based on only one species is exceptionally justifiable, and he mentions *E. cinnaberinus* (Olivier 1789; a former partial synonym of *E. kollari*) as such an exception in this sense. All in all, our study aims to preserve the last remaining populations of the ladybird spider in northwest Germany.

Figure 1.—The study area in the nature reserve Lüneburger Heide, northwest Germany. In the foreground: heather with small open patches and a pitfall trap (marked by a flag).

METHODS

Study species.—*Eresus kollari* belongs to the cribellate spider family Eresidae (Platnick 2011). Male and female spiders of this species spend most of their lives underground in their well-camouflaged tube webs. The adults live in a burrow of about 1 cm diameter and a maximum depth of 10 cm. The spider weaves parts of leaves from the surrounding plants into the burrow's roof directly above the ground, making the web almost invisible throughout most of the year. It can only be found during 2 wk in May when the females strengthen the threads of the webs to catch prey for their offspring (Baumann 1997).

Males mature at the age of 2.5 yr, whereas females mature at 3–4 yr (Baumann 1997). Only males leave the burrow to mate at the end of their lives for a period of ~ 2 wk between August and October. In their nuptial dress, they search for females within a diameter of ~ 10–12 m. Males and females share precisely the same habitat, and both show a very low dispersal potential (Baumann 1997).

Study area.—The study area (Fig. 1) is situated in the nature reserve Lüneburger Heide about 6 km east of Schneverdingen (53°7′43N, 09°52′45E). The nature reserve includes the most extensive heathlands of northwest Germany, covering an area of ~ 5,000 ha. Niemeyer et al. (2007) characterize the climate of the nature reserve as a humid suboceanic type with a mean annual precipitation of 811 mm and a mean annual temperature of 8.4° C. They describe the soil as Pleistocene sandy deposits and nutrient-poor podzols or podzolic soils, pH range 3.2–3.6. Old, high heather shrubs covered the whole study site at least from the 1960s to the 1980s (Lütkepohl 1993). Since 2002, the last year in which the heather was mown, management practices have halted (Mertens pers. comm.).

Our study was carried out in 2007. The study area was subdivided into three parts in which we placed 100 pitfall traps. Part A (100 by 130 m, 60 traps) appeared fairly homogenous and consisted mainly of young, low heather plants with open patches, lichens, and moss. Part B (140 by 200 m, 30 traps), directly adjoining Part A, consisted of older heather, mainly 50–100 cm height, and interspersed with birch trees. Part C (10 traps, 5 in the forest and 5 in the grassland area), 400 m distant from part B, was an area of coniferous forest and forest edge with high grass scattered with young trees. All pitfalls were placed in rows, each holding 10 traps.

Sampling and predictor variables.—We applied a stratified random sampling approach to sample species occurrence and environmental data (cf. Hirzel & Guisan 2002). Direct observation of individuals or webs would be the best method to record species occurrence in the field. However, as the webs are difficult to find, we used pitfall trapping instead.

As female and male spiders share exactly the same habitat and stay in their webs during their whole life spans, our data can be applied to both sexes, although our information is only based on capture of males. They only leave their burrows at the end of their lives to search for females in close vicinity of their burrows (Bellmann 1997; Baumann 1997).

From 14 August 2007 to 16 October 2007, during the mate-searching period of the males, we used 100 pitfall traps. Plastic, 10 cm diam. cups were used, covered with a piece of netting wire to prevent larger animals from falling in. The

traps were filled with a mixture of 50% ethanol, 20% glycerine, and 30% water (modified after Renner 1982) as a preservative. The traps were emptied fortnightly. Nineteen environmental variables were recorded from each trap location. Habitat structure strongly influences the occurrence of spider species (cf. Schwab et al. 2002; Ziesche & Roth, 2008), so we thus selected and analyzed the variables that describe the habitat in terms of temperature, moisture, and structure. The vegetation cover of the dominant vascular plant species in different vegetation layers was estimated within a diameter of 1 m around each trap.

We analyzed vegetation cover in 3 different layers a) 0–10 cm, b) 10–50 cm, c) > 50 cm, estimating the percentage cover of the main vegetation components like *Calluna vulgaris* and/or *Erica tetralix* as well as grasses, lichens, bare soil, moss, and trees. Additionally, we measured the thickness of the organic layer (cm). We also collected the data of the temperature of the top soil and the soil at 10 cm depth (° C). Insolation (Lux) and temperature (° C) data were taken separately on 5 September, a sunny day, over midday by means of a photometer and a digital thermometer with a 10-cm-long metal rod. We took a spadeful of soil sample of every trap to measure the pH-value (pH_{H2O}), organic matter content (%), and water content (%) of the A-horizon.

Statistical analysis.—To estimate the occurrence probabilities of *E. kollari* depending on environmental predictor variables, we used two different approaches: logistic regression as a standard parametric approach and boosted regression trees (BRT), a promising, non-parametric ensemble forecasting technique (cf. Elith et al. 2008). To achieve the best balanced predictive model, we used P_{fair} as the appropriate classification threshold (according to Schröder & Richter 1999). The threshold P_{fair} ensures that sensitivity (= percentage of correctly predicted presences) and specificity (= percentage of correctly predicted absences) of the model have the same magnitude.

For our logistic regression analysis, we first performed univariate logistic regressions for each of the predictor variables, following the approach of Hosmer & Lemeshow (2000). Only predictors with $P < 0.25$ in the univariate logistic regression were considered as potential candidates for multiple regression analysis. Significance in the logistic regression model was assessed using the likelihood ratio test. To assess correlation between predictors, we analyzed their bivariate correlation structure. None of the potential candidates showed a bivariate correlation stronger than $r_s = 0.553$ (Spearman rank-correlation test). Within the multiple regression model, we also tested the significance of two-way interaction terms and quadratic terms for each of the previously selected predictors. None of the interaction terms and only one of the quadratic terms (moss layer in herbage cover) was significant ($P < 0.05$), but this is not considered in the final model. From the resulting set of predictors, we deleted those with a significance level of $P > 0.1$ from this model. In a further step, backwards stepwise selection ('fastbw': Harrell 2001) was used to prove the importance of the predictors left in the final model. This method uses the fitted complete model and computes approximate Wald statistics by computing conditional (restricted) maximum likelihood estimates, assuming multivariate normality of estimates.

Nagelkerke's R^2 was used for evaluating model calibration. To assess model discrimination and performance, we used the program ROC_AUC provided by Schröder (2006) to calculate the AUC (area under a receiver operating characteristic curve: Swets 1988) and some threshold-dependent criteria such as the correct classification rate and Cohen's kappa. To quantify the total independent contribution of the single predictors considered in the logistic regression, we ran a hierarchical partitioning procedure (MacNally 2000; Heikkinen et al. 2005; Müller et al. 2009; Schröder et al. 2009).

Habitat models run the risk of being overfitted to the training data (Harrell 2001; Steyerberg et al. 2001; von dem Bussche et al. 2008). As independent data were not available to correct for this optimism, we used bootstrapping with 100 replicates to correct the measures of model performance (e.g., Peppler-Lisbach & Schröder 2004; Oppel et al. 2004). This method allows almost unbiased estimates of model performance and was found to provide the best estimate of internal validity of predictive logistic regression models (Reineking and Schröder 2003; Schröder 2008).

To compare these results with a more flexible non-parametric approach, we also built boosted regression trees (BRT, see Elith et al. 2008 for details). This approach combines the boosting algorithm (Schapire & Singer 1999) with classification and regression trees (De'ath & Fabricius 2000), leading to a set of several hundreds or thousands of trees in the final model (De'ath 2007). It has the advantage that it allows for an implicit modeling of thresholds as well as interactions between predictors. BRTs were estimated with a tree complexity of 5 and a learning rate of 0.001. Variable selection was performed in a forward stepwise manner, so that only important predictors are considered in the final model. The approach makes it possible to calculate the contributions of all predictors in explaining the variability of the response variable. Model performance in terms of AUC and Nagekerke's R^2_N was evaluated based on tenfold cross-validation. For both methods, residuals were checked for spatial autocorrelation by calculating global Moran's I (Dormann et al. 2007) and spline correlograms (Bjørnstad & Falck 2001; Schröder 2008).

We carried out the statistical analyses with R 2.7.1 (R Development Core Team 2008). Hierarchical partitioning was conducted using the 'hier.part'-library (version 1.0, MacNally & Walsh 2004), and the 'Hmisc' (version 3.0-12) and 'Design' library (version 2.0-12) (Harrell 2001) were used for the logistic regression procedure. The library 'gbm' (provided by G. Ridgeway, supported by some functions provided by J. Elith and J. Leathwick) was used for boosted regression tree modeling. Response curves of logistic regressions were plotted using the program LR-mesh provided by Rudner (2004). Spatial autocorrelation was checked by applying the library 'spdep' (Bivand 2006).

RESULTS

In total, 95 *E. kollari* specimens, all of which were males, were found in 48 of the 100 pitfalls. In 26 traps, we found only one individual of the studied species, with a maximum of six found in two of the traps. In part A of the study site, spiders fell into 41 of 60 traps. We observed positive spatial autocorrelation in the raw presence-absence data within a

Table 1.—Parameter estimates of the multiple logistic regression model explaining the occurrence of *E. kollari* (residual deviance = 104.90 on 96 degrees of freedom, null devianee = 138.47 on 99 degrees of freedom). Significance values for each coefficient were obtained from Wald tests. Although not significant at $\alpha = 0.05$, β_3 was left in the model because of its contribution to the model evaluated with Wald statistics in the stepwise backwards selection of variables.

Variable	Regression coefficient	*SE*	Wald Z	*P*
β_1 Soil temperature at 10 cm depth	0.591	0.226	2.61	0.009
β_2 Thickness of organic layer	−0.360	0.159	−2.27	0.023
β_3 *Calluna*/*Erica* cover in herb layer	0.015	0.009	1.71	0.087
β_0 Intercept	−8.420	3.556	−2.37	0.018

50 m distance from each trap (partial Moran's I statistic standard deviate = 9.119, $P < 0.001$).

Habitat variables related to species presence.—The final logistic regression model considers three predictors with a strong effect on occurrence probability (Table 1). 'Thickness of organic layer' ($R^2_N = 0.28$ in a univariate regression, $P < 0.001$) had a negative effect on the occurrence probability of *E. kollari*. In contrast, 'soil temperature at 10 cm depth' ($R^2_N = 0.22$, $P < 0.001$), and '*Calluna* cover in herb layer' ($R^2_N = 0.15$, $P < 0.01$) both had a positive effect (Fig. 2). At our study site, these variables covered a large gradient, range of 12.4–17.3° C in soil temperature and range of 0–12 cm in the thickness of the organic layer, whereas the height of *Calluna* reached 8–50 cm and its soil coverage was 3–100%. Occurrence probabilities of 50% are explained by a minimum soil temperature of 15° C and a maximum organic layer of 3 cm (Figs. 2, 3).

The final logistic regression model explained a considerable proportion of the overall variance in our dataset ($R^2_N = 0.38$). A first model containing predictors that were associated with the outcome of the final model ($P < 0.25$, according to Hosmer & Lemeshow 2000) explained slightly more variance in our dataset ($R^2_N = 0.44$), but some predictors were removed ('heather in herb layer,' the cover of 'herbage in moss and herb layer,' 'soil temperature on surface,' 'intensity of light on surface') in the stepwise model selection process for the final model.

In order to quantify the independent contribution of the predictor variables considered in both the logistic regression and the BRT model, we conducted a hierarchical partitioning analysis. The results for the logistic regression model show the relatively high influence of the organic layer (44.0%). The independent effect of soil temperature at 10 cm depth was also quite high (35.5%), whereas the cover of heather in the herb layer had an independent effect of 20.5%.

Soil temperature at 10 cm depth (27.6%) and thickness of the organic layer (22.6%) best explained the variability of the response variable in the BRT model. Other variables such as soil water content, insolation, heather cover in the herb layer, and proportion of organic matter in the soil contributed

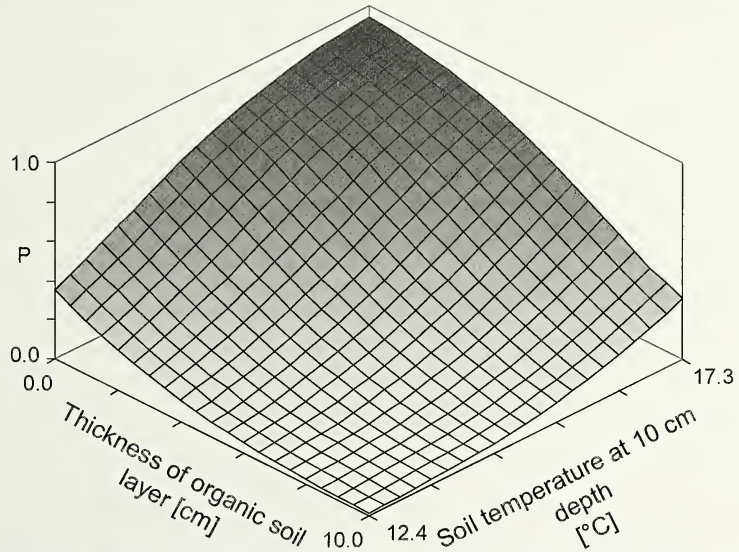


Figure 2.—Bivariate response surface of the two most important predictors in the final logistic regression model (see Table). The estimated occurrence probability (P) of *E. kollari* is plotted against the two continuous predictors.

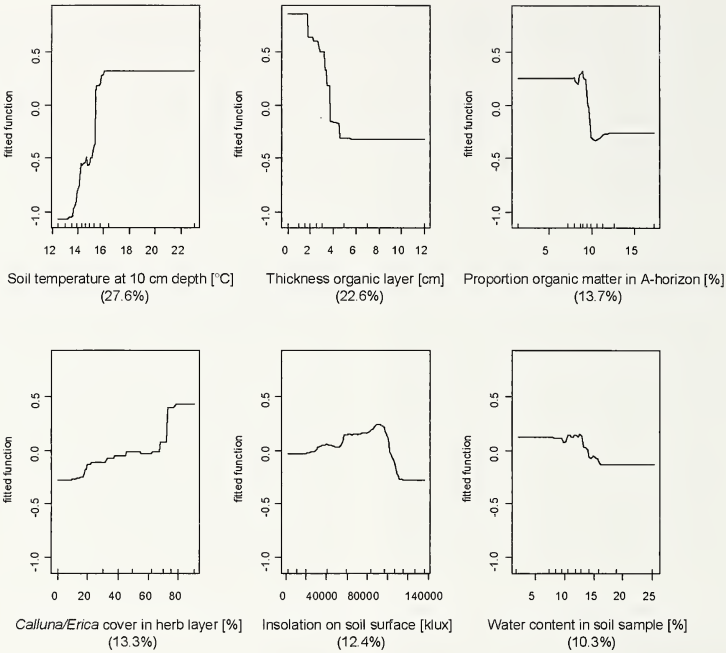


Figure 3.—Univariate response curves of the six most influential variables derived from the BRT model: Soil temperature at 10 cm depth; thickness of organic layer; proportion of organic matter in A-horizon; *Calluna/Erica* cover in herb layer; insolation on soil surface; water content in soil sample. The relative influence of each variable in the model is given in parentheses.

between 10.3 and 13.7% to the variability in the response variable (Fig. 3).

Model performance and validation.—The logistic regression model showed a relatively good discriminative power with an AUC-value of 0.80 ($CI_{95\%}$: 0.72–0.89). Using P_{fair} in the model, we reached a correct classification rate of 75%. The evaluation of Cohen's kappa indicates good predictive power for our final model. Internal validation by bootstrapping revealed only slight overfitting of the final model. Corrected values were R^2_N = 0.34 and AUC-value = 0.78, which indicates acceptable discriminative performance. This shows that our model is robust within the study site.

Accordingly, the BRT model reached an AUC = 0.80 and R^2_N = 0.253 after tenfold cross-validation and an apparent model performance of AUC = 0.91 ($CI_{95\%}$: 0.85–0.96) and R^2_N = 0.53, CCR = 0.81 and kappa = 0.62. Neither the logistic regression (Moran's I statistic standard deviate = 0.068, P = 0.473) nor the BRT approach (Moran's I statistic standard deviate = 0.929, P = 0.176) showed any residual spatial autocorrelation.

DISCUSSION

Our study describes the ecological demands of this spider species in the last remaining heathland areas in Germany. Our logistic regression model indicates that the occurrence of *E. kollari* in the large heathland complex of northwest Germany is influenced primarily by the three habitat variables. Here we discuss the effect of each variable.

1) There was a negative effect of the thickness of the organic layer. The layer functions as an obstacle to the male's locomotory behavior in the sense of spatial resistance (Duffey 1962). This means that the management measures should strive to maintain a rather thin organic layer of maximum 3 to 4 cm. This is of great importance not only for males, since both sexes have to penetrate the organic layer in order to dig their burrows (Baumann 1997).

2) The models showed a positive effect of temperature at 10 cm depth, but not at the surface. This is likely due to the fact that the males, like the females, spend nearly all their lives in burrows dug in soil. This variable may affect the occurrence of females rather than males, since females prefer higher temperature places for quick development of brood (cf. Klein et al. 2005).

The soil surface temperature fluctuated from trap to trap. This variable was excluded by the automatic model selection procedure for the logistic regression model, but had an explanatory power of 12.4% in the boosted regression trees (Fig. 3). Hence, the occurrence of the males during the vagrant period (Baumann 1997) is less influenced by the surface temperature than by the soil temperature deeper in the ground.

3) Both models demonstrated that '*Calluna* cover in the herb layer' also has a fairly strong influence (with 13.3% in the BRT-model) on the occurrence of the species. However, our models cannot distinguish between the influence of *Calluna* cover in the herb layer and the importance of the moss layer. Other authors have pointed out that *Eresus* prefers wind-protected sites (Wiehle 1953; Bellmann 1997; Baumann 1997). This may explain why *E. kollari* prefers sites in which heather is higher than 10 cm but lower than 50 cm, since this vegetation height allows enough wind-shelter, but also provides sufficient insolation to reach the required temperature at a depth of 10 cm. Hence, *E. kollari* can be considered as a stenotopic thermophilic species of dry heathlands.

Our statistical models revealed habitat variables that can be used to predict the occurrence of *E. kollari* with a correct classification rate ranging from 75 up to 83% and with considerable discriminative power. Since we built a predictive distribution model based on presence and absence data from trapping in the field, the circumstances under which AUC could be a misleading performance measure do not apply to our study (Lobo et al. 2008). Higher AUC scores can likely be obtained by increasing the geographical extent of models (Lobo et al. 2008) because of the larger environmental distances of the absences. Nevertheless, the results of the distribution model presented here are limited to the predictors used and, to some extent, to the location from which the data were obtained. Internal validation revealed only slight overfitting, but further analysis is necessary to determine whether the model is generally applicable to other regions. In general, both the BRT and the logistic regression model seem to be robust (bootstrapping) within the investigated study site.

As *E. kollari* was not found in 19 of the 60 pitfall traps in the most suitable part of our study site (part A), we assume that it could follow the metapopulation dynamics reported from other arthropod stenotopic heathland species (Habel et al. 2007; Assmann & Janssen 1999; Drees et al. 2011). This may also be the reason why our statistical models do not explain more than 38% of the occurrence of *E. kollari* on our study site.

The dispersal power of *E. kollari* is too low to colonize or recolonize empty habitat patches, at least under the conditions of the highly fragmented heathland patches in the nature reserve Lüneburger Heide (cf. Eggers et al. 2010). Baumann (1997) proved low dispersal power by marking 1,004 individuals of *Eresus*. Recaptures showed that this species has a very poor dispersal potential, since the offspring build their new burrows in close proximity to their mother's web. Baumann's studies on males have shown that spatial resistance is of great importance to these animals; thus, males do not move farther than 10 to 12 m on average from their own burrows. The farthest distance moved by a single spider was 61 m.

Therefore, both low dispersal power and the spatially structured populations, as indicated by positive spatial autocorrelation within the first 50 m around occurrences, should result in a decline of the species if heathland areas are strongly fragmented. This decline has already been recognized (Platen et al. 1998; Blick et al., in press). Proof of the existence of non-occupied, though suitable patches for an *Eresus* species has already been given by a successful transfer experiment in England with *E. sandaliatus*, a sibling species of *E. kollari* (Hughes et al. 2009). This result can be best explained by a metapopulation structure in *E. sandaliatus*.

Conclusions for a sound conservation strategy.—Due to both the spatially structured populations and the probable existence of unoccupied habitat patches, we recommend re-introduction experiments with *E. kollari* to habitat patches that seem to belong to the same type of patches. Monitoring of the re-introduction effort is also strongly recommended.

Three main variables (thickness of the organic layer, soil temperature at 10 cm depth, *Calluna* cover in the herb layer) have been shown to be decisive for the occurrence of the ladybird spider. Based on these variables, we recommend the implementation of an elaborated management plan that guarantees long-term heathland quality (cf. McFerran et al. 1995; Bell et al. 2001) and can accommodate the habitat requirements of *E. kollari*:

1) Choppering is a management measure that creates bare soil by removing the above-ground biomass and most parts of the O-layer, with only a thin layer of organic material remaining on the surface (Niemeyer et al. 2007). It promotes the heterogeneity of heathland soil by removing the small ridges and maintaining the micro-relief. Thus, after being choppered, the raw-humus layer would offer a huge variety of suitable combinations of the variables 'organic layer' and '*Calluna* coverage' suggested by our habitat model. In part A of our study area, the last heathland management measure, 'mulch mowing,' took place in 2002. Mowing, too, seems to be an appropriate measure for conservation of the *E. kollari* population and probably also for other European *Eresus* species on different sites (Usher 1992; Bell et al. 2001).

2) We also recommend prescribed burning, since it leaves the temperatures unchanged at a depth of a few centimeters so that it cannot harm the spider in its tube webs; the whole process also leaves the micro-relief untouched (McFerran et al. 1995; Niemeyer et al. 2005). The structure after burning might also provide appropriate habitat. However, the raw humus layer required by E. *kollari* will only be restored after several years. Grasses (e.g., *Molinia careulea*) regenerate after prescribed burning, but break down only after the second year (Niemeyer et al. 2005; Härdtle et al. 2009).

Usher (1992) suggests that the habitats of such a rare species as *Eresus kollari* should be managed throughout Europe. As a basic principle, if management measures are not applied in heathlands, it will not be possible to ensure the long-term preservation of this habitat (Usher 1992; Härdtle et al. 2007). For choppering, we recommend that a pattern of strips or a fishbone-structure should be employed in *E. kollari* conservation measures, so that the spiders have the chance to move from the untouched colonized habitat patches into the managed areas in order to colonize or recolonize empty habitat patches. The measures should be applied at a distance of a maximum of 50 m as well. We would recommend that the strips should be not broader than the machine used, and the patches chosen for choppering should be narrow enough to allow the spider to move over. It is also very important to leave some time (ca 5 yr) after the measures have been carried out for the development or redevelopment of these sites, and to spread the measures cyclically and periodically in space and time.

Our knowledge of the effects of management measures on arthropod fauna is still poor, and long-term studies are only available for ground beetles in the Netherlands (den Boer & van Dijk 1995). These studies report that some endangered species, typical for heathlands, benefit from burning and choppering (or, in some cases, sod cutting). The only known long-term study of the dynamics of heathland spider species does not refer to the effects of habitat management (Gajdoš & Toft 2000). Only long-term monitoring (over at least 10 years) will be able to show what impact the management measures recommended as a result of our habitat suitability model will have on the endangered spider species *E. kollari*.

ACKNOWLEDGMENTS

We are grateful to the Verein Naturschutzpark e.V., especially to Dirk Mertens, for assisting us with his expert knowledge in the field, and to the Alfred Toepfer Academy (NNA) for permission to collect the samples in the nature reserve. Furthermore, we thank Dr. Thomas Niemeyer, Leuphana University Lueneburg, for fruitful discussions and hints regarding heathland ecology and measures.

LITERATURE CITED

Assmann, T. 1999. The ground beetle fauna of ancient and recent woodlands in the lowlands of north-west Germany (Coleoptera, Carabidae). Biodiversity and Conservation 8:1499–1517.

Assmann, T. & J. Janssen. 1999. The effects of habitat changes on the endangered ground beetle *Carabus nitens* (Coleoptera: Carabidae). Journal of Insect Conservation 3:107–116.

Assmann, T., W. Dormann, H. Främbs, S. Gürlich, K. Handke, T. Huk, P. Sprick & H. Terlutter. 2003. Rote Liste der in Niedersachsen und Bremen gefährdeten Sandlaufkäfer und Laufkäfer mit Gesamtverzeichnis. Informationsdienst Naturschutz Niedersachsen 23(2):70–95.

Baumann, T. 1997. Populationsökologische und zönotische Untersuchungen von Habitatqualität und Habitatfragmentierung für Spinnenpopulationen auf Trockenrasen am Beispiel von *Eresus cinnaberinus* (Oliv. 1789). Dissertation, University of Bremen. Wissenschaft und Technik Verlag, Berlin.

Bell, J.R., C.P. Wheater & W.R. Cullen. 2001. The implications of grassland and heathland management for the conservation of spider communities: a review. Journal of Zoology 255:377–387.

Bellmann, H. 1997. Kosmos Atlas Spinnentiere Europas. Kosmos, Stuttgart.

Binzenhöfer, B., B. Schröder, R. Biedermann, B. Strauss & J. Settele. 2005. Habitat models and habitat connectivity analysis for butterflies and burnet moths – the example of *Zygaena carniolica* and *Coenonympha arcania*. Biological Conservation 126:247–259.

Binzenhöfer, B., R. Biedermann, J. Settele & B. Schröder. 2008. Connectivity compensates for low habitat quality and small patch size in the butterfly *Cupido minimus*. Ecological Research 23:259–269.

Bivand, R. 2006. Implementing spatial data analysis software tools. R. Geography Analysis 38:23–40.

Bjørnstad, O.N. & W. Falck. 2001. Nonparametric spatial covariance functions: estimation and testing. Environmental and Ecological Statistics 8:53–70.

Blick, T., P. Bliss, R. Drogla, O. Finch, M. Gerisch, A. Haenggi, K.H. Harms, J. Kiechle, C. Komposch, A. Malten, D. Martin, C. Muster, D. Nährig, R. Platen, I. Roedel, P. Sacher, M. Scheidler, A. Schoenhofer, A. Staudt, H. Stumpf & D. Tolke. In press. Rote Liste der Spinnen Deutschlands (Arachnida: Araneae). Status March 2008.

Buse, J., B. Schröder & T. Assmann. 2007. Modelling habitat and spatial distribution of an endangered longhorn beetle - A case study for saproxylic insect conservation. Biological Conservation 137:372–381.

Desender, K., M. Dufrêne & J.P. Maelfait. 1994. Long term dynamics of carabid beetles in Belgium: a preliminary analysis on the influence of changing climate and land use by means of a database covering more than a century. Pp. 247–252. *In* Carabid Beetles - Ecology and Evolution. (K. Desender, M. Dufrêne, M. Loreau, M.L. Luff & J.P. Maelfait, eds.). Kluwer, Dordrecht.

De'ath, G. & K.E. Fabricius. 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. Ecology 81:3178–3192.

De'ath, G. 2007. Boosted trees for ecological modeling and prediction. Ecology 88:243–251.

Den Boer, P.J. & T.S. van Dijk. 1995. Carabid beetles in a changing environment. Wageningen Agricultural University Papers 94:1–30.

Dormann, C.F., J.M. McPherson, M.B. Araújo, R. Bivand, J. Bolliger, G. Carl, R. Davis, A. Hirzel, W. Jetz, W.D. Kissling, I. Kühn, R. Ohlemüller, P.R. Peres-Neto, B. Reineking, B. Schröder, F.M. Schurr & R. Wilson. 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data. Ecography 30:609–628.

Drees, C., H. de Vries, W. Härdtle, A. Matern, M. Persigehl & T. Assmann. 2011. Genetic erosion in a stenotopic heathland ground beetle (Coleoptera: Carabidae): a matter of habitat size? Conservation Genetics 12:105–117.

Duffey, E. 1962. A population study of spiders in limestone grassland. Journal of Animal Ecology 31:571–599.

Eggers, B., A. Matern, C. Dress, J. Eggers, W. Härdtle & T. Assmann. 2010. Value of semi-open corridors for simultaneously connecting open wooded habitats: a case study with ground beetles. Conservation Biology 24:256–266.

Elith, J., J.R. Leathwick & T. Hastie. 2008. A working guide to boosted regression trees. Journal of Animal Ecology 77:802–813.

Finch, O.D. 2004. Rote Liste der in Niedersachsen und Bremen gefährdeten Webspinnen (Araneae). Informationsdienst Naturschutz Niedersachsen 24(5):1–20.

Gajdoš, P. & S. Toft. 2000. A twenty-year comparison of epigeic spider communities (Araneae) of Danish coastal heath habitats. Journal of Arachnology 28:90–96.

Gimingham, C.H. 1972. Ecology of Heathlands. Chapman & Hall, London.

Habel, J.C., T. Schmitt, W. Härdtle, M. Lütkepohl & T. Assmann. 2007. Dynamics in a butterfly-plant-ant system: influence of habitat characteristics on turnover rates of the endangered lycaenid *Maculinea alcon*. Ecological Entomology 32:536–543.

Härdtle, W., T. Niemeyer, T. Assmann, H. Meyer & G. von Oheimb. 2007. Can prescribed burning compensate for atmospheric nutrient loads in wet heathlands? Phytocoenologia 37:161–174.

Härdtle, W., O. von Oheimb, A.-K. Gerke, M. Niemeyer, T. Niemeyer, T. Assmann, C. Drees, A. Matern & H. Meyer. 2009. Shifts in N and P budgets of heathland ecosystems: effects of management and atmospheric inputs. Ecosystems 12:298–310.

Harrell, F.E. 2001. Regression Modeling Strategies. Springer, New York.

Heikkinen, R.K., M. Luoto, M. Kuussaari & J. Pöyry. 2005. New insights into butterfly–environment relationships using partitioning methods. Proceedings of the Royal Society - Biological Science B 272:2203–2210.

Hein, S., J. Voss, H.-J. Poethke & B. Schröder. 2007. Habitat suitability models for the conservation of thermophilic grasshoppers and bush crickets. Journal of Insect Conservation 11:221–240.

Heisswolf, A., S. Reichmann, H.-J. Poethke, B. Schröder & E. Obermaier. 2009. Habitat quality matters for the distribution of an

endangered leaf beetle and its egg parasitoid in a fragmented landscape. Journal of Insect Conservation 13:165–175.

Hirzel, A. & A. Giusan. 2002. Which is the optimal strategy for habitat suitability modelling? Ecological Modelling 157:331–341.

Hosmer, D.W. & S. Lemeshow. 2000. Applied Logistic Regression. Wiley, New York.

Hughes, I., R. Key, P. Merrett, A. Nicholson & D. Heaver. 2009. The Ladybird Spider in Britain – its history, ecology and conservation. British Wildlife 20:153–159.

Johannesen, J. & M. Veith. 2001. Population history of *Eresus cinnaberinus* (Araneae: Eresidae) colour variants at a putative species transition. Heredity 87:114–124.

Keienburg, T., J. Prüter, W. Härdtle, T. Kaiser, A. Koopmann, A. Melber, F. Niemeyer & S. Schaltegger. 2004. Feuer und Beweidung als Instrumente zur Erhaltung magerer Offenlandschaften in Nordwestdeutschland. NNA-Berichte 17(2):3–12.

Keienburg, T. & J. Prüter. 2004. Conservation and Management of Central European Lowland Heathlands. Case Study: Lüneburger Heide Nature Reserve, North-West Germany. Heathguard, The Heathland Centre, Lygra, Norway.

Klein, B.A., T.C. Bukowski & L. Avilés. 2005. Male residency and mating patterns in a subsocial spider. Journal of Arachnology 33:703–710.

Kuhk, R. & W. Rabeler. 1956. *Eresus niger* (Pet.), Araneina, auf norddeutschen Zwergstrauchheiden. Steiniger, Natur und Jagd in Niedersachsen, Hannover, 211–214.

Lobo, J.M., A. Jimenez-Valverde & R. Real. 2008. AUC: a misleading measure of the performance of predictive distribution models. Global Ecology and Biogeography 17:145–151.

Lütkepohl, M. 1993. Schutz und Erhaltung der Heide. Leitbilder und Methoden der Heidepflege im Wandel des 20. Jahrhunderts am Beispiel des Naturschutzgebietes Lüneburger Heide. NNA-Berichte 6(3):10–20.

MacNally, R. 2000. Regression and model-building in conservation biology, biogeography and ecology: the distinction between – and reconciliation of – 'predictive' and 'explanatory' models. Biodiversity and Conservation 9:655–671.

MacNally, R. & C.J. Walsh. 2004. Hierarchical partitioning public-domain software. Biodiversity and Conservation 13:659–660.

Maes, D. & H. Van Dyck. 2005. Habitat quality and biodiversity indicator performances of a threatened butterfly versus a multispecies group for wet heathlands in Belgium. Biological Conservation 123:177–187.

McFerran, D.M., J.H. McAdam & W.I. Montgomery. 1995. The impact of burning and grazing of heathland plants and invertebrates in country Antrim. Biology and Environmental-Proceedings of the Royal Irish Academy 95B:1–17.

Matern, A., C. Drees & M. Kleinwächter. 2007. Habitat modelling for the conservation of the rare ground beetle species *Carabus variolosus* (Cololeoptera, Carabidae) in the riparian zones of headwaters. Biological Conservation 136:618–627.

Müller, J., J. Pöllath, R. Moshammer & B. Schröder. 2009. Predicting the occurrence of middle spotted woodpecker *Dendrocopos medius* on a regional scale, using forest inventory data. Forest Ecology Management 257:502–509.

Niemeyer, M., T. Niemeyer, S. Fottner, W. Härdtle & A. Mohamed. 2007. Impact of sod-cutting and choppering on nutrient budgets of dry heathlands. Biological Conservation 134:344–353.

Niemeyer, T., M. Niemeyer, A. Mohamed, S. Fottner & W. Härdtle. 2005. Impact of prescribed burning on the nutrient balance of heathlands with particular reference to nitrogen and phosphorus. Applied Vegetation Science 8:183–192.

Oppel, S., H.M. Schaefer, V. Schmidt & B. Schröder. 2004. Habitat selection by the pale-headed brush-finch, *Atlapetes pallidiceps*, in southern Ecuador: implications for conservation. Biological Conservation 118:33–40.

Platen, R., T. Blick, P. Sacher & A. Malten. 1996. Rote Liste der Webspinnen Deutschlands (Arachnida: Araneae). Arachnologische Mitteilungen 11:5–31.

Peppler-Lisbach, C. & B. Schröder. 2004. Predicting the species composition of mat-grass communities (Nardetalia) by logistic regression modelling. Journal of Vegetation Science 15:623–634.

Platnick, N.I. 2011. The World Spider Catalog, Version 11.5. The American Museum of Natural History, New York. Online at http://research.amnh.org/iz/spiders/catalog/INTRO1.html.

R Development Core Team. 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Online at http://www.R-project.org.

Reineking, B. & B. Schröder. 2003. Computer-intensive methods in the analysis of species-habitat relationships. Pp. 165–182. *In* Gene Bits und Ökosysteme - Implikationen neuer Technologien für die ökologische Theorie. (H. Reuter, B. Breckling & A. Mitwollen, eds.), Theorie in der Ökologie, Volume 9. Peter Lang, Frankfurt am Main.

Renner, K. 1982. Coleopterenfänge mit Bodenfallen am Sandstrand der Ostseeküste, ein Beitrag zum Problem der Lockwirkung von Konservierungsmitteln. Faunistisch-ökologische Mitteilungen 5:137–146.

Řezáč, M., S. Pekár & J. Johannesen. 2008. Taxonomic review and phylogenetic analysis of central European *Eresus* spiders (Araneae: Eresidae). Zoologica Scripta 37:263–287.

Rudner, M. 2004. LR-Mesh - Response surfaces for logistic regression models. Computer program, version 1.0.5. Online at http://www.uni-oldenburg.de/landeco/21343.html

Schapire, R.E. & Y. Singer. 1999. Improved boosting algorithms using confidence-rated predictions. Mach Learn 37:297–336.

Schröder, B. & O. Richter. 1999. Are habitat models transferable in space and time? Zeitschrift fur Ökologie und Naturschutz 8:195–205.

Schröder, B. 2006. ROC & AUC-Calculation – evaluating the predictive performance of habitat models. Online at http://brandenburg.geoecology.uni-potsdam.de/users/schroeder/download.html

Schröder, B. 2008. Challenges of species distribution modeling below ground. Journal of Plant Nutrition and Soil Seience 171:325–337.

Schröder, B., B. Strauss, R. Biedermann, B. Binzenhöfer & J. Settele. 2009. Predictive species distribution modeling in butterflies. *In* Ecology of Butterflies in Europe. (J. Settele, T.G. Shreeve, M. Konvicka & H. van Dyck, eds.). Cambridge University Press, Cambridge, UK.

Schwab, A., D. Dubois, P.M. Fried & P.J. Edwards. 2002. Estimating the biodiversity of hay meadows in north-eastern Switzerland on the basis of vegetation structure. Agriculture Ecosystems & Environment 93:197–209.

Steyerberg, E.W., M. Eijkemans & J. Habbema. 2001. Application of shrinkage techniques in logistic regression analysis: a case study. Statistica Neerlandica 55:76–88.

Swets, J.A. 1988. Measuring the accuracy of diagnosis systems. Science 240:1285–1293.

The Council of the European Communities. 2004. Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora - Consolidated Text. Office for Official Publications of the European Communities.

Usher, M.B. 1992. Management and diversity of arthropods in *Calluna* heathland. Biodiversity and Conservation 1:63–79.

Völksen, G. 1993. Die Entstehung der Kulturlandschaft, Lüneburger Heide". NNA-Berichte 6(3):4–10.

von dem Bussche, J., R. Spaar, H. Schmid & B. Schröder. 2008. Modelling the recent and potential future spatial distribution of ring ouzel (*Turdus torquatus*) and blackbird (*T. merula*) in Switzerland. Journal of Ornithology 149:529–544.

Webb, N.R. 1998. The traditional management of European heathlands. Journal of Applied Ecology 35:987–990.

Wiehle, H. 1953. Spinnentiere oder Arachnoidea (Araneae) IX: Orthognatha – Cribellatae – Haplogynae – Entelegynae. Pp. 70–75. *In* Die Tierwelt Deutschlands, 42. Teil. (F. Dahl, ed.). VEB Gustav Fischer, Jena.

Ziesche, M. & M. Roth. 2008. Influence of environmental parameters on small-scale distribution of soil-dwelling spiders in forests: what makes the difference, tree species or microhabitat? Forest Ecology and Management 255:738–752.

Manuscript received 15 September 2010, revised 11 March 2011.

2011. The Journal of Arachnology 39:393–398

Vertical distribution of spiders in soil

Vratislav Laška[1], **Oldřich Kopecký**[2], **Vlastimil Růžička**[3], **Jan Mikula**[1], **Adam Véle**[4], **Bořivoj Šarapatka**[1] and **Ivan H. Tuf**[1,5]: [1]Department of Ecology and Environmental Sciences, Faculty of Science, Palacký University Olomouc, Svobody 26, 77146 Olomouc, Czech Republic; [2]Department of Zoology and Fish Farming, Faculty of Agrobiology, Food and Natural Resources, Czech University of Life Sciences in Prague, Kamýcká 129, Praha 6 - Suchdol 165 21, Czech Republic; [3]Institute of Entomology, Biology Centre, AS CR, Branišovská 31, 37005 České Budějovice, Czech Republic; [4]Forestry and Game Management Research Institute Jíloviště-Strnady, Frýdek-Místek Office, Nádražní 2811, 73802 Frýdek-Místek, Czech Republic

Abstract. Research studies of the shallow subterranean habitats as environments for arthropods have been sparse up to this point. Using subterranean traps, we studied the distribution of spiders in soil profile over a depth span of 5–95 cm at six sites. Although almost 40% of individual specimens (1088 in total) were obtained from the epigeon (5 cm depth), spiders colonized all parts of the soil profiles examined. Beside ground-dwelling species with significant preferences for the upper layers, some species (*Porrhomma microphthalmum* (O. Pickard-Cambridge 1871), *Centromerus cavernarum* (L. Koch 1872), *Cicurina cicur* (Fabricius 1793), *Dysdera lantosquensis* Simon 1882, and *Nesticus cellulanus* (Clerck 1757)) commonly inhabited the whole range of the profiles studied, without any depth preference. In contrast, depigmented and microphthalmous *Porrhomma microps* (Roewer 1931) and *Maro* sp. exclusively inhabited deep soil layers adjoining void systems in bedrock.

Keywords: Mesovoid shallow substratum, superficial underground compartment, subterranean environment, Araneae

The soil is an aphotic environment inhabited by casual transmigrants as well as fauna adapted for subterranean life (e.g., microphthalmy, depigmentation etc.). Soil porosity limits the size of its inhabitants; nevertheless, soil spaces vary in dimension from sand fissures to cave systems (Christian 1999). Three distinct types of habitats in relation to the soil can be formally distinguished: 1) epigean, inhabited by surface dwelling animals; 2) endogean, with mainly edaphic animals; and 3) hypogean, with subterranean species inhabiting void systems, including caves (Giachino & Vailati 2010).

Our knowledge of endo- and hypogeic animals is limited, due to difficulties in collecting samples. Invertebrates inhabiting a subterranean environment can be studied with the use of only a few methods. One such method is the use of pitfall traps, modified in various ways (e.g., a collar around the nose, perforation of walls), dug to different depths and exposed for an extended period of time (Růžička 1982, 1988; Yamaguchi & Hasegawa 1996). Another type is Barber's Shingle Trap (Barber 1997), with bait inside and a long hose exposed at the depth studied. A frequently used method involves traps installed in drills (Illie 2003; Illie et al. 2003; Negrea 2004). One clever modification of drill trapping is the subterranean trap designed by Schlick-Steiner and Steiner (2000) that collects animals in one drill at various depths.

Beside an extensive knowledge of cave spiders (e.g., Paquin & Dupérré 2009), we have some information on spiders in scree slopes (Růžička et al. 1995; Růžička 1999a, 1999b, 2002; Růžička & Klimeš 2005). In stony alpine debris, spiders are generally most abundant in the upper layers, but differ significantly depending on locality (Schlick-Steiner & Steiner 2000). A similar pattern of abundance was found in the vertical distribution of spiders in peat bogs (Biteniekytė & Rėlys 2006). However, we have limited knowledge about spiders inhabiting soil, as endogeic and hypogeic spiders have only been studied recently in Bulgaria (Deltshev et al. 2011). The present study aims to reveal whether spiders inhabit deep soil layers and to characterize the vertical distribution of spider communities at several sites with different soil types in Central Europe.

[5]Corresponding author. E-mail: ivan.tuf@upol.cz

METHODS

Site description.—The research was carried out at six sites in the Czech Republic; three of them (*Above cave, Rock, Debris*) were situated in Central Moravia near the town of Hranice na Moravě (320 m a.s.l.). The other three sites (*Beech wood, Quarry, Valley*) were situated 10 km east of the town of Skuteč, on the border of Ždárské vrchy Protected Landscape Area (Eastern Bohemia, approx. 450 m a.s.l.).

Above cave (49°31′N, 17°44′E)*:* This site is situated above Zbrašov Aragonite Caves. The cave system is linked with stony debris above through shafts, ending approximately one meter below the surface. The upper soil layer was covered by leaf litter from deciduous forest. The debris was partially filled by soil particles created by interskeletal erosion forming lithosol soil type.

Rock (49°32′N, 17°44′E)*:* This site is one kilometer from *Above cave* under a limestone rock face in deciduous forest. In this renzic leptosol soil type, the upper organic layer is about 5 cm thick, the A-horizon with a mixture of organic and inorganic particles (about 15 cm thick) passing to the C-horizon with broken-down lime bedrock (stones several centimeters in diameter) and clay.

Debris (49°32′N, 17°44′E)*:* This site is only about 50 m from the *Rock* site on a slope in deciduous forest. The soil is similar to the previous one, but with larger stones (20–30 cm).

Beech wood (49°50′N, 16°3′E)*:* This site with cambisol soil type has a thick layer of leaf litter covering an A-horizon (ca 15 cm) passing to a 50 cm-thick cambic horizon above arenaceous marl bedrock.

Table 1.—List of spider species in subterranean traps, with the number of trapped specimens and their depth range (uppermost to undermost record). Nomenclature of spiders according to Platnick (2010) with two exceptions: *Dysdera lantosqueusis* sensu Řezáč et al. (2008) and *Porrhomma microps* (= *lativelum*) sensu Růžička (2009).

Family / Species	# Specimens	Depth distribution
Dysderidae		
Dysdera lantosquensis Simon 1882	25	5–95 cm
Harpactea lepida (C.L. Koch 1838)	101	5–95 cm
Harpactea rubicunda (C.L. Koch 1838)	3	5–15 cm
Nesticidae		
Nesticus cellulanus (Clerck 1757)	28	5–85 cm
Theridiidae		
Pholcomma gibbum (Westring 1851)	14	5–95 cm
Robertus lividus (Blackwall 1836)	13	5–35 cm
Robertus truncorum (L. Koch 1872)	2	15 cm
Linyphiidae		
Asthenargus perforatus Schenkel 1929	1	15 cm
Bathyphantes gracilis (Blackwall 1841)	1	5 cm
Centromerus cavernarum (L. Koch 1872)	28	5–75 cm
Centromerus silvicola (Kulczyński 1887)	37	5–55 cm
Ceratinella brevis (Wider 1834)	16	5–15 cm
Diplocephalus picinus (Blackwall 1841)	5	5–25 cm
Diplostyla concolor (Wider 1834)	7	5–15 cm
Entelecara acuminata (Wider 1834)	1	55 cm
Maro sp.	2	45–65 cm
Micrargus herbigradus (Blackwall 1854)	5	5–15 cm
Microneta viaria (Blackwall 1841)	6	5 cm
Neriene emphana (Walckenaer 1841)	1	25 cm
Oedothorax apicatus (Blackwall 1850)	223	5–55 cm
Palliduphantes alutacius (Simon 1884)	83	5–95 cm
Porrhomma microphthalmum (O. Pickard-Cambridge 1871)	185	5–85 cm
Porrhomma microps (Roewer 1931)	21	25–85 cm
Porrhomma oblitum (O. Pickard-Cambridge 1871)	1	15 cm
Saaristoa firma (O. Pickard-Cambridge 1905)	1	25 cm
Saloca diceros (O. Pickard-Cambridge 1871)	15	5–95 cm
Tenuiphantes flavipes (Blackwall 1854)	21	5–35 cm
Tenuiphantes tenebricola (Wider 1834)	1	5 cm
Walckenaeria atrotibialis (O. Pickard-Cambridge 1878)	2	5 cm
Walckenaeria dysderoides (Wider 1834)	1	15 cm
Walckenaeria furcillata (Menge 1869)	3	5–15 cm
Walckenaeria obtusa Blackwall 1836	2	5 cm
Walckenaeria vigilax (Blackwall 1853)	5	15 cm
Araneidae		
Araneus diadematus Clerck 1757	1	5 cm
Lycosidae		
Trochosa terricola Thorell 1856	2	25–35 cm
Agelenidae		
Histopona torpida (C.L. Koch 1834)	7	5–85 cm
Malthonica silvestris (L. Koch 1872)	6	5–65 cm
Cybaeidae		
Cybaeus angustiarum L. Koch 1868	8	5–75 cm
Hahniidae		
Hahnia nava (Blackwall 1841)	1	25 cm
Dictynidae		
Cicurina cicur (Fabricius 1793)	123	5–95 cm
Amaurobiidae		
Amaurobius fenestralis (Ström 1768)	2	5 cm
Callobius claustrarius (Hahn 1833)	2	5–15 cm
Coelotes terrestris (Wider 1834)	9	5–25 cm
Eurocoelotes inermis (L. Koch 1855)	12	5 cm
Liocranidae		
Apostenus fuscus Westring 1851	5	5–15 cm
Clubionidae		
Clubiona brevipes Blackwall 1841	3	5 cm
Salticidae		
Ballus chalybeius (Walckenaer 1802)	3	5 cm
Neon reticulatus (Blackwall 1853)	9	15–25 cm

Quarry (49°50′N, 16°2′E): This site was situated in an abandoned basalt quarry. The soil profile consisted entirely of pieces of basalt about 10 cm in size. The upper soil layers, including vegetation, were removed during excavation.

Valley (49°50′N, 16°2′E): This site is ca 1 km from the preceding one, situated in the Krounka stream basin. This debris slope is covered by deciduous forest and large stones overgrown with mosses. The homogenous soil profile comprised of basalt stones is about 20–25 cm in size with space partially filled by organic material from trees and inorganic particles created by erosion to a depth of one meter.

Sampling.—Spiders were collected using subterranean traps (Schlick-Steiner & Steiner 2000). The trap, made of rigid plastic, consists of a tube (10 cm in diameter) with three fissures (ca 4 mm wide, 6–7 cm long) at 10 cm intervals. The traps are over one meter long, and the last sampling fissure was 95 cm deep. A hole, about 1.5 × 0.7 m and 1.3 m deep was dug at each site, and soils of different layers were separated carefully using plastic sheets. Three tubes were put in the hole in line with each other, 50 cm apart, and the hole was then filled with soil in the proper order. A set of ten removable plastic containers (250 ml) situated on a central metal axis was placed in each tube; the position of the containers corresponded to the fissures in the tube. Through this arrangement, the containers collected animals entering the tube through fissures at particular depths. The traps were filled with a 4%

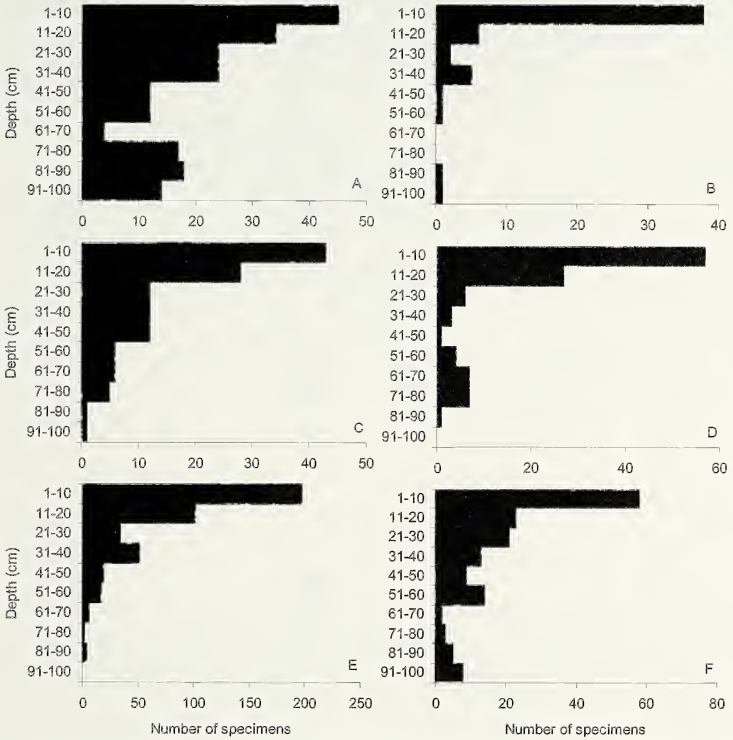


Figure 1.—Depth distribution of spider individuals at sites studied (number of all collected specimens). A – *Above cave* (altogether 205 individuals, 17 spp.), B – *Rock* (55 individuals, 12 spp.), C – *Debris* (126 individuals, 20 spp.), D – *Beech wood* (113 individuals, 17 spp.), E – *Quarry* (433 individuals, 9 spp.), F – *Valley* (156 individuals, 18 spp.).

formaldehyde solution and emptied at six-week intervals between 7 March 2005 and 17 March 2007. Voucher specimens are deposited in the collection of V. Růžička at the Institute of Entomology, Biology Centre, AS CR in České Budějovice.

Data analysis.—In the analysis, we used only species with more than 10 individuals and/or species found in more than four sites. RDA (Canonical redundancy analysis) was used to study the effect of depth and individual site. The significance of the first axis was determined by a Monte Carlo permutation test (499 permutations). Data standardized by error variance were used for RDA. Generalized linear models (GLM) with Poisson errors were used to study the relationship of each species and environmental variables (site, depth). CANOCO software was used for these analyses (Ter Braak, Šmilauer 1998).

RESULTS

The most numerous taxa collected were Collembola (44.7%), followed by Diptera (13.0%), Oniscidea (12.5%), Coleoptera (10.8%), Araneae (10.0%), and other rare taxa (Diplopoda 2.7%, Acarina 2.0%, Chilopoda 1.3%, Pseudoscorpiones 1.1%, Formicidae 0.8%, Dermaptera 0.6%, and Opiliones 0.4% respectively). Altogether, 1088 spider specimens of 48 species were trapped (Table 1). Among 14 spider families, the Linyphiidae was the richest in species (26 species), followed by the Amaurobiidae (4 species), Theridiidae and Dysderidae (3 species each) and Agelenidae and Salticidae (2 species each). We only evaluated the distribution of the 17 most numerous species statistically.

Quarry was the site with the greatest number of trapped spiders (433 individuals, 9 species); the highest number of species was recorded at *Debris* (20 species). The most numerous catches were in the upper level, at a depth of 5 cm (almost 40% of the individuals), and the lowest were at a depth of 95 cm (2.5%). Beside the most abundant spiders at the uppermost level, no common pattern was typical for all sites (Fig. 1). The number of spider species below 55 cm was highest in the *Above cave* site (over 30%), followed by *Debris*, *Beech wood*, and *Valley* sites (about 20%), followed by *Rock* and *Quarry* sites (only approximately 6%).

The RDA model revealed significant differences among the distribution of species ($F = 9.07$, $P < 0.01$). The sum of all

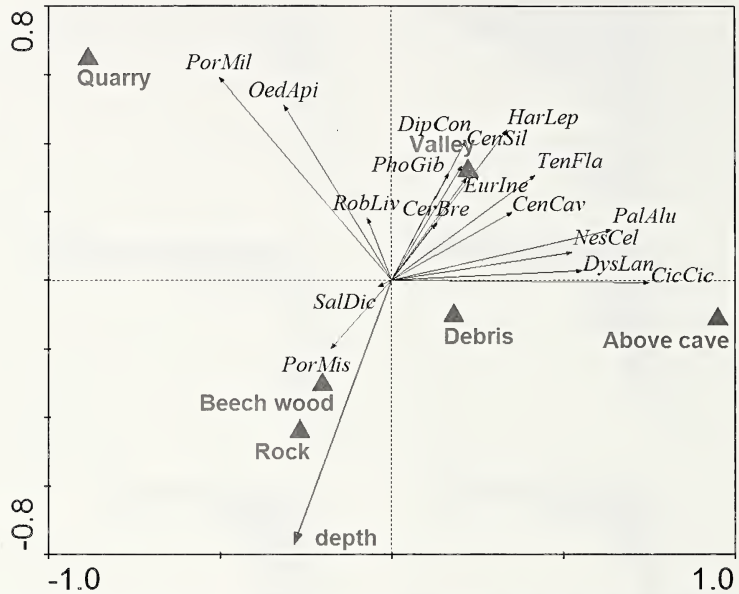


Figure 2.—RDA ordination biplot illustrating distribution of spiders in relation to sites and depth. Abbreviations: CenCav – *Centromerus cavernarum*, CenSil – *Centromerus silvicola*, CerBre – *Ceratinella brevis*, CicCic – *Cicurina cicur*, DipCon – *Diplostyla concolor*, DysLan – *Dysdera lantosquensis*, EurIne – *Eurocoelotes inermis*, HarLep – *Harpactea lepida*, NesCel – *Nesticus cellulanus*, OedApi – *Oedothorax apicatus*, PalAlu – *Palliduphantes alutacius*, PhoGib – *Pholcomma gibbum*, PorMil – *Porrhomma microphthalmum*, PorMis – *Porrhomma microps*, RobLiv – *Robertus lividus*, SalDic – *Saloca diceros*, TenFla – *Tenuiphantes flavipes*.

canonical eigenvalues explains 50.7% of variability. Although there is no common pattern of depth distribution of spiders, depth is a significant general predictor ($F = 7.74$, $P < 0.01$), and distribution patterns and community compositions differ among sites ($F = 3.18$, $P = 0.04$). The ordination diagram shows that *Porrhoma microps* (Roewer 1931) is positively correlated with soil depth (Fig. 2).

GLM modeling of the response of the 17 dominant spider species to depth showed significant pattern for ground-dwelling species mainly; the spiders inhabiting the entire profile do not significantly prefer any depth (Table 2). These 17 species can be separated into four categories according to their depth distribution and preferences (distributions of 11 species with more than 20 trapped specimens are displayed in Fig. 3):

1. Exclusively surface dwelling species: *Eurocoelotes inermis* (L. Koch 1855), *Diplostyla concolor* (Wider 1834), *Ceratinella brevis* (Wider 1834)
2. Surface-dwelling species (significant preference for upper layers) penetrating into deeper layers: *Centromerus silvicola* (Kulczyński 1887), *Oedothorax apicatus* (Blackwall 1850), *Tenuiphantes flavipes* (Blackwall 1854), *Harpactea lepida* (C.L. Koch 1838), *Robertus lividus* (Blackwall 1836), *Palliduphantes alutacius* (Simon 1884), *Saloca diceros* (O. Pickard-Cambridge 1871)
3. Species inhabiting whole soil profile (without preference for any depth): *Pholcomma gibbum* (Westring 1851), *Porrhomma microphthalmum* (O. Pickard-Cambridge 1871), *Centromerus cavernarum* (L. Koch 1872), *Cicurina cicur* (Farricius 1793), *Dysdera lantosquensis* Simon 1882, *Nesticus cellulanus* (Clerck 1757)
4. Species inhabiting exclusively (any) of the deeper layers: *Porrhomma microps*. Two other species, too rare for statistical evaluation, were found in the deeper layers: *Entelecara acuminata* (Wider 1834) at 55 cm and *Maro* sp. at 45 cm and 65 cm (identification is complicated by expanded palps; these two specimens have slightly reduced eyes, unlike species of *Maro*, posterior median eyes 1.2 diameters apart).

DISCUSSION

Studies of the deep soil layer environment have been scarce due to the difficulty of sampling these arthropod communities. We present evidence for the occurrence of spiders (invertebrates larger than typical soil invertebrates such as mites and collembolans) in soil layers down to one meter in depth.

Vertical distribution of spiders in the soil profile differed according to the habitat type. Although we were not able to evaluate the soil porosity due to the presence of large stones (making it impossible to take intact soil samples), we assume that there were relatively large spaces at some study sites (e.g., in fractured, arenaceous marl bedrock). This seems to be an important factor for the vertical distribution of spiders.

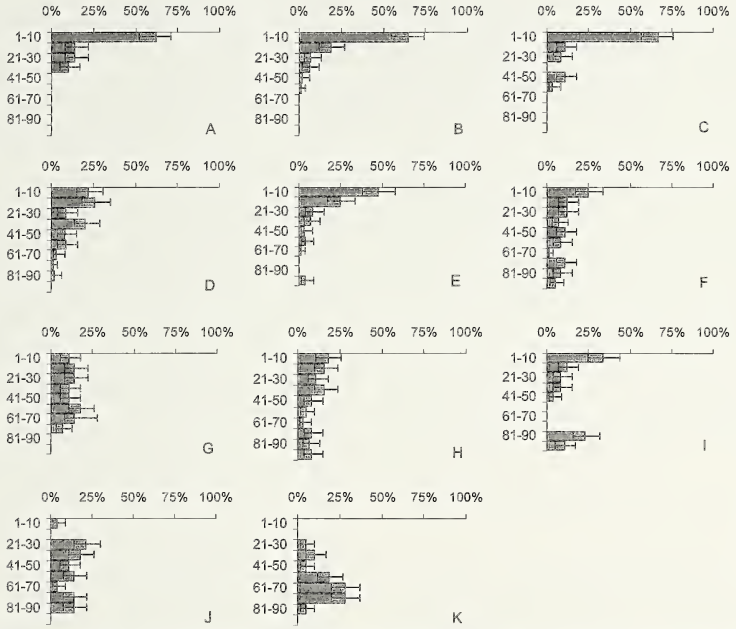


Figure 3.—Depth distribution of 11 species (more than 20 trapped specimens apiece). Bars represent mean proportions, whiskers are 95% confidence intervals. A – *Tenuiphantes flavipes* (mean record at 12 cm), B – *Oedothorax apicatus* (mean record at 11 cm), C – *Centromerus silvicola* (mean record at 10 cm), D – *Porrhomma microphthalmum* (mean record at 27 cm), E – *Harpactea lepida* (mean record at 19 cm), F – *Palliduphantes alutacius* (mean record at 38 cm), G – *Centromerus cavernarum* (mean record at 39 cm), H – *Cicurina cicur* (mean record at 40 cm), I – *Dysdera lantosquensis* (mean record at 40 cm), J – *Nesticus cellulanus* (mean record at 48 cm), K – *Porrhomma microps* (mean record at 61 cm).

Spiders were found to inhabit deeper soil layers in scree slopes with large soil spaces (*Above cave*, *Debris*, *Valley*, *Beech wood*, Fig. 1). Spiders were less common in the deeper soil layers in sites with small spaces and small stones. The *Beech wood* site was a different case, hosting spiders in the deep soil layer, which likely did not penetrate it from the surface. Spiders found here were microphthalmous species that can inhabit the subterranean environment created by systems of voids (MSS) in arenaceous marl bedrock exclusively. Presence of MSS is evident at sites *Above Cave* (corresponding with cave environment) and also *Valley* (Fig. 1).

Several species exhibit a clear tendency to live in deep soil layers. These belong to the families Linyphiidae, Dictynidae, and Nesticidae. Small body size results in a large ratio of surface area to volume, and vulnerability of desiccation. The deeper layers of soil can protect these individuals against desiccation. Such a pattern was described by Wagner et al. (2003) in the litter at a microscale level.

An affinity to a broad spectrum of subterranean habitats is found in species of the genus *Porrhomma*. A species recorded in this study, *P. microps*, has been repeatedly found in caves in Italy and in leaf litter in Germany (Růžička 2009). Although it also inhabits leaf litter in floodplain forests of the Czech Republic (Buchar & Růžička 2002), it was also recently found

Table 2.—Categorization of species by their affinity to depth and results of GLM model (Note: only values related to depth are presented).

Species	Category	*F*	*P*
Ceratinella brevis	1	3.78	0.03
Diplostyla concolor	1	24.91	< 1.0e-6
Eurocoelotes inermis	1	20.18	< 1.0e-6
Centromerus silvicola	2	5.12	0.01
Harpactea lepida	2	12.56	0.00
Oedothorax apicatus	2	3.51	0.04
Palliduphantes alutacius	2	3.62	0.03
Robertus lividus	2	4.71	0.01
Saloca diceros	2	3.17	0.05
Tenuiphantes flavipes	2	13.93	0.00
Centromerus cavernarum	3	1.75	0.18
Cicurina cicur	3	1.45	0.24
Dysdera lantosquensis	3	2.21	0.12
Pholcomma gibbum	3	2.97	0.06
Porrhomma microphthalmum	3	2.06	0.14
Nesticus cellulanus	3	0.96	0.39
Porrhomma microps	4	1.67	0.20

in karst and pseudokarst caves. *Porrhomma egeria* Simon 1884 was recorded in basalt scree slopes at a depth of about 1 m (Růžička et al. 1995) and in the block accumulations and crevice caves in a decaying gneiss massif at depths greater than 5 m (Růžička 1996). A troglomorphic population of *Porrhomma myops* Simon 1884 was recorded in caves and in andesite scree slopes at a depth of 40–100 cm (Růžička 2002), whereas an edaphomorphic population of this species was described from a deep soil layer (35–95 cm) in floodplain forest (Růžička et al. 2011). *Porrhomma microcavense* Wunderlich 1990 was recorded in an arenaceous marl layer (Kůrka et al. 2006). This rock is known to form extensive underground void systems, and we consider these void systems to be ideal locations for the future research of invertebrates in shallow subterranean habitats. This assumption is supported by a record of microphthalmous *Maro* sp. in a beech forest on arenaceous marl bedrock during our research.

Another species, *Zangherella relicta* (Kratochvíl 1935) (Anapidae) was described from caves in Montenegro, and recently it was found at several localities in Bulgaria, where it occurs exclusively in mountain scree slopes at depths of 40–50 cm (Deltshev et al. 2011). All these findings document individual phases of the evolutionary process leading to colonization of subterranean environment over the entire depth profile of the terrain (Růžička 1999a; Culver & Pipan 2009; Giachino & Vailati 2010).

ACKNOWLEDGMENTS

We hereby wish to thank G. Hormiga (George Washington University, Washington, D.C.) for his help with the identification of *Maro* species. The project was partially supported by the Ministry of Education, Youth, and Sport of the Czech Republic (IRP MSM 6046070901 and G4-2350/2008), by the National Research Program II (2B 06101), and by the Ministry of Agriculture of the Czech Republic (0002070203). We also wish to thank two anonymous reviewers and in particular the editor for valuable comments.

LITERATURE CITED

Barber, A.D. 1997. A simple shingle trap for myriapods. Bulletin of the British Myriapod Group 13:27–28.

Biteniekytė, M. & V. Rėlys. 2006. Investigation of activity and vertical distribution of spiders in *Sphagnum* tussocks of peat bogs. Biologija 1:77–82.

Buchar, J. & V. Růžička. 2002. Catalogue of Spiders of the Czech Republic. Peres, Praha.

Christian, E. 1999. From sand fissures to cave systems – subterranean biology in Austria. Pp. 121–126. *In* Lebensraum Blockhalde – Zur Ökologie periglazialer Blockhalden im ausseralpinen Mitteleuropa. (B.M. Möseler & R. Molenda, eds.). Decheniana – Beihefte (Bonn).

Culver, D.C. & T. Pipan. 2009. Superficial subterranean habitats – gateway to the subterranean realm? Cave and Karst Science 35:5–12.

Deltshev, C., S. Lazarov, M. Naumova & P. Stoev. 2011. A survey of spiders (Araneae) inhabiting the eudaphic soil stratum and the superficial underground compartment in Bulgaria. Arachnologische Mitteilungen 40:33–46.

Giachino, P.M. & D. Vailati. 2010. The Subterranean Environment. Hypogean Life, Concepts and Collecting Techniques. WBA Handbooks, Verona.

Ilie, V. 2003. Chilopoda species from the edaphic and subterranean environments of the Cloşani karstic area (Romania). Travaux du Muséum National d' histoire Naturelle "Grigore Antipa" 45:129–137.

Ilie, V., Ş. Negrea & B. Mitić. 2003. The diversity of the Chilopoda species from the karstic area of the Anina mountains (Banat, Romania). Archives of Biological Sciences, Belgrade 55:93–99.

Kůrka, A., J. Buchar, L. Kubcová & V. Bryja. 2006. Spiders (Araneae) of Kokořínsko Protected Landscape Area. Bohemia Centralis 27:91–135.

Negrea, Ş. 2004. On the Chilopoda from south-eastern Dobrogean karstic area (Romania). 3. The material collected using deep traps placed in drillings and artificial microcaves. Travaux du Muséum National d' histoire Naturelle "Grigore Antipa" 47:111–128.

Paquin, P. & N. Dupérré. 2009. A first step towards the revision of *Cicurina*: redescription of type specimens of 60 troglobitic species of the subgenus *Cicurella* (Araneae: Dictynidae), and a first visual assessment of their distribution. Zootaxa 2002:1–67.

Platnick, N.I. 2010. The World Spider Catalog, version 10.5. American Museum of Natural History, New York. Online at http://research.amnh.org/entomology/spiders/catalog/index.html.

Řezáč, M., J. Král & S. Pekár. 2008. The spider genus *Dysdera* (Araneae, Dysderidae) in central Europe: revision and natural history. Journal of Arachnology 35:432–462.

Růžička, V. 1982. Modifications to improve the efficiency of pitfall traps. Newsletter of the British Arachnological Society 34:2–4.

Růžička, V. 1988. The longtimely exposed rock debris pitfalls. Acta Societatis Zoologicae Bohemicae 52:238–240.

Růžička, V. 1996. Species composition and site distribution of spiders (Araneae) in a gneiss massif in the Dyje river valley. Revue Suisse de Zoologie, vol. hors serie, 561–569.

Růžička, V. 1999a. The first steps in subterranean evolution of spiders (Araneae) in Central Europe. Journal of Natural History 33:255–265.

Růžička, V. 1999b. The freezing scree slopes and their arachnofauna. Pp. 141–148. *In* Lebensraum Blockhalde – Zur Ökologie periglazialer Blockhalden im ausseralpinen Mitteleuropa. (B.M. Möseler & R. Molenda, eds.). Decheniana – Beihefte (Bonn).

Růžička, V. 2002. Spatial distribution of spiders (Araneae) on scree slopes in Křivoklátsko and Moravský Kras Protected Landscape Areas. Acta Societatis Zoologicae Bohemicae 66:321–328.

Růžička, V. 2009. The European species of the *microphthalmum*-group in the genus *Porrhomma* (Araneae: Linyphiidae). Contributions to Natural History 12:1081–1094.

Růžička, V., J. Hajer & M. Zacharda. 1995. Arachnid population patterns in underground cavities of a stony debris field (Araneae, Opiliones, Pseudoscorpionidea, Acari: Prostigmata: Rhagidiidae). Pedobiologia 39:42–51.

Růžička, V. & L. Klimeš. 2005. Spider (Araneae) communities of scree slopes in the Czech Republic. Journal of Arachnology 33:280–289.

Růžička, V., V. Laška, J. Mikula & I.H. Tuf. 2011. Morphological adaptations of *Porrhomma* spiders (Araneae: Linyphiidae) inhabiting soil. Journal of Arachnology 39:355–357.

Schlick-Steiner, B.C. & F.M. Steiner. 2000. Eine neue Subterranfalle und Fänge aus Kärnten. Carinthia II 190:475–482.

Ter Braak, C.J.F. & P. Šmilauer. 1998. CANOCO Reference Manual and User's Guide to Canoco for Windows: Software for Canonical Community Ordination (version 4). Microcomputer Power, Ithaca, New York.

Wagner, J.D., S. Toft & D.H. Wise. 2003. Spatial stratification in litter depth by forest-floor spiders. Journal of Arachnology 31:28–39.

Yamaguchi, T. & M. Hasegawa. 1996. An experiment on ant predation in soil using a new bait trap method. Ecological Research 11:11–16.

Manuscript received 15 August 2009, revised 9 May 2011.

2011. The Journal of Arachnology 39:399–408

Developmental response to low diets by giant *Nephila clavipes* females (Araneae: Nephilidae)

Linden Higgins and **Charles Goodnight**: Department of Biology, University of Vermont, Burlington Vermont 05405 USA. E-mail: Linden.Higgins@uvm.edu

Abstract. Female-biased sexual size dimorphism is common in arthropods, apparently driven by fecundity selection in females. Selective pressures that limit growth are less often considered. One factor that researchers have rarely considered is the possible role of energetic limits on growth. The orb weaving spider *Nephila clavipes* (Linnaeus 1767) is extremely sexually size dimorphic. Males are "normal" sized spiders and females are up to ten times longer, having passed through several additional juvenile instars. This extreme size dimorphism presents the opportunity to test for intrinsic energetic costs of gigantism. Prior studies have shown that males successfully reach maturity on a range of diets, while female dietary requirements increase rapidly with increasing size. We here examine the effects of variation in food availability on juvenile female development by randomly assigning spiderlings from six different families (from six distinct populations) to quantitatively varying but qualitatively identical diets. Based upon field observations, we expected that dietary restrictions would have the greatest effect on duration of instars, particularly later instars, and on instar number (because longer total development would lead to curtailment of growth at an earlier stage), with relatively little effect on growth per molt. Because the diets ranged from higher than mean intake observed in the field to well below mean intake, we expected females to mature at a wide range of instars (and sizes). Our results support the functional relationship among food intake, instar duration, and fixed growth per molt (although growth per molt was less canalized than suggested by field observations). However, we observed no variation in number of instars, and we suggest that these data provide additional support for the importance of rare, large prey in the diets of web-building spiders.

Keywords: Phenotypic plasticity, rare large prey hypothesis, survivorship

"Reverse" sexual size dimorphism (SSD) is generally believed due to fecundity selection (Darwin 1871); female arthropods commonly show size-dependent fecundity, where larger or heavier females lay many more eggs (e.g., Miyashita 1986; Higgins 1992a, 2002; Legrand & Morse 2000; Uhl et al. 2004; Fernandez-Montraveta & Moya-Larano 2007). But there must be countervailing selection against continued increases in female size. Proposed selective pressures against larger size include selection for early maturation (e.g., Roff 2001; however, see Berner & Blanckenhorn 2007), selection against developmental asynchrony when males are much smaller than females (Calabrese et al. 2008; L. Higgins & C. Goodnight pers. obs.), and selection imposed by the increased energetic requirements of increased size (Higgins 2002; Higgins & Goodnight 2010).

In *Nephila*, as in most spiders, development is determinant; there are no molts subsequent to the molt to sexual maturity. Age and size at sexual maturity reflect the interaction of juvenile development with the environment (Higgins & Rankin 1996; Berner & Blankenhorn 2007). Size at sexual maturity is determined by growth per molt, which shows little variation in the field (Higgins 1992a, 1993) and the total number of instars (Higgins and Rankin 1996). Age at sexual maturity is determined by the time spent in each instar and the number of instars. *Nephila clavipes* (Linnaeus 1767) females are several instars larger than their male siblings, and juvenile females require accelerating amounts of food, quantities that are an increasing proportion of their mass rather than a constant proportion of their mass (Higgins & Goodnight 2010). Males, maturing in roughly half the number of juvenile stages compared to their female siblings, have a much greater likelihood of reaching maturity under conditions of food stress (L. Higgins & C. Goodnight unpubl. results).

In addition to the energetic constraints that juvenile females may experience, field observations also indicate that females are under different temporal selective regimes than males. The total development time required for females can approach the length of the growing season in many habitats (Higgins 2000), and males develop so much earlier than females that late-maturing females may not be able to find mates (Higgins 1989).

We therefore expect late instar juvenile females to respond very strongly to dietary limitation, and moreover predict, based upon field observations, that instar duration and instar number will vary more than growth per molt. To test our model of developmental responses to diet, we reared *N. clavipes* females on diets that are adequate for young juvenile development and male maturation (Higgins & Rankin 2002; L. Higgins & C. Goodnight pers. obs.). Here we report on the developmental consequences of quantitatively different diets, ranging from relatively poor to more rich than most field observations. The diet treatments were qualitatively identical, consisting of the same prey items in the same proportions. Our analyses include comparison of laboratory growth to field growth and tests for family and dietary influences on juvenile development.

METHODS

We set out to test our predictions by rearing spiders of six Mexican families of the large orb-weaving species *Nephila clavipes* on three quantitatively different diets, all within the range of mean daily prey capture observed in the field. All diets were qualitatively identical and consisted of prey that have been used to rear other spider species successfully, including other *Nephila* (Mayntz et al. 2003; Fernandez-Montraveta & Moya-Larano 2007; N. Ruppel & J. Schneider pers. com.; M. Elgar & L Ceballos pers. com.).

Table 1.—Collecting locations for *Nephila clavipes*. All are in Veracruz except Tolosita, Oaxaca.

Name	Location	Altitude	Seasonality
Nanciyaga	18°27′N, 95°4′W	< 50 m	long wet/warm versus dry/cool
Quihuitztlan	19°40′N, 96°25′W	170 m	long wet/warm versus dry/cool
Fortín de las Flores	18°54′N, 96°60′W	990 m	short wet/warm versus dry/cold
Xalapa	19°30′N, 96°53′W	1000 m	short wet/warm versus dry/cold
Sayula de Alemán	17°52′N, 94°59′W	80 m	long wet/warm versus dry/warm
Tolosita	17°12′N, 95°2′W	50 m	long wet/warm versus dry/warm

***Nephila clavipes* natural history.**—*Nephila* is a relatively small genus of pantropical orb-weaving spiders (Kuntner et al. 2008). Extreme sexual size dimorphism due to the evolution of female gigantism is ancestral to the genus (Kuntner & Coddington 2009). There is a great deal of variation among species in mean size and variation in size (Higgins et al. in press), and male size and female size are evolving independently (Kuntner & Coddington 2009). The source populations for the laboratory experiments are all assumed to be univoltine. Spiders reproduce late in the growing season, females laying up to five egg sacs on or under leaves. All surviving females die with the onset of drought or winter conditions (Higgins 2000), and late females may fail to copulate (Higgins 1989) or may not have time to produce an egg sac (Higgins 2000). The spiderlings hatch and molt within the egg sac, and over-winter as first or second instars. Emergence is triggered in the field by unknown cues, likely a combination of warmth and moisture in most habitats.

Nephila clavipes has determinant growth, and no molts follow maturation. Males in the penultimate instar can be identified due to swelling of their pedipalps, but prior to that point they cannot be distinguished from juvenile females. All but two males in these experiments had entered the penultimate stage by the eighth instar (two delayed to the ninth instar), so we assume that all eighth instar spiders lacking pedipalp swelling are females. The dark, heavily sclerotized epigynal plate near the genital opening indicates female maturity.

We collected mature, gravid females in the fall of 2006 from six Mexican populations (Table 1; voucher specimens housed at the National Museum of Natural History, Smithsonian Institution). These sites span a range of environmental conditions, and represent six populations with low levels of gene flow (J. Nuñez pers. com.). The populations chosen for study fall into three pairs of similar environmental and climate conditions: lowland tropics (Nanciyaga, Quihuitztlan), mid-altitude temperate tropics (Xalapa, Fortín) and lowland seasonally dry tropics (Sayala, Tolosita). Xalapa and Fortín are always univoltine (Higgins 2000; P. Berea pers. com.) and Nanciyaga is usually univoltine (Higgins 2000). Sayala and Tolosita we believe to be univoltine due to the climate similarity between these sites and Chamela, which is univoltine (Higgins 2000; www.tutiempo.net/clima/ accessed 5 March 2009).

Spider rearing.—Mature females collected in the late summer were maintained in the laboratory (ca 75% RH, 10:14 L:D, ca 27° C) on a diet of crickets (fed dog food and apples) and houseflies (from SpiderPharm.com; maintained after maturity on sugar and dry milk with water available from a sponge). We kept the egg sacs laid by these females under the same conditions until hatching and first molt (which happens inside the egg sac). They were then moved to "winter" conditions (10:14 L:D, 4° C for the temperate populations or 16° C for lowland populations; humidity maintained by damp toweling that was checked bi-weekly) for 5–10 weeks to stagger emergence of spiderlings. Due to the logistical difficulties of individually feeding spiderlings on controlled diets, only spiders from one haphazardly chosen egg sac from each population were included in these experiments.

When we were ready to add additional spiders to the experiment, we moved an egg sac into warm conditions (Percival incubator, 75% RH, 14:10 L:D, 27° C). Upon the spiders' emergence and molting to the third instar [leg 1 tibia + patella (TPL) ca 0.1 cm], we placed spiderlings into individual boxes (11 cm wide × 11 cm high × 4 cm deep) with 2.5 cm or 5.1 cm chicken wire for web supports and randomly assigned to a diet treatment (Table 2). We increased food levels by 50% when spiders molted to the sixth instar because prior results indicated that juvenile dietary requirements increase greatly about this stage of development (Higgins & Goodnight 2010).

As the spiders grew, we moved them into larger boxes to accommodate their larger webs: once when they molted to TPL ≥ 0.3 cm (22 cm wide × 10 cm high × 10 cm deep) and again when they molted to TPL ≥ 0.7 cm (31 cm wide × 23.5 cm high × 11 cm deep, Pioneer plastics). All but three males reached sexual maturity prior to TPL = 0.6 cm. To mimic declining day length in natural habitats, all spiders were moved to short-day conditions (11:13h L:D) in a walk-in chamber approximately 100 days after starting the experimental treatment (101 ± 2 days). Most males were sexually mature at the time of the move. Temperature and humidity in the walk-in chamber were less exactly controlled, but averaged 24° C and 72% RH.

We fed all spiders twice weekly, at which time we recorded and removed all uneaten dead flies and recorded if the spider had molted. We recorded size as leg 1 tibia-patella length (TPL) because this is easily and reliably measured without

Table 2.—Feeding regimes for spiders. Weekly food levels as percent of spider mass. * Diet determined individually based on post-molt size at each instar. † Size ranges overlap because spiders on lower diets sometimes grew less per molt, and qualitative diet shifts were established by instar not by size.

Instar(s)	Size range (TPL, cm)†	Quantity of food as percent spider mass			Diet quality (ratio by mass)
		L	M	H	
3–5	0.1–0.45	35	56	84	*D. melanogaster*
6*	0.46–0.80	56	84	126	*D. melanogaster*:*D. virilis* (4:6)
7*	0.70–0.93	56	84	126	*D. virilis*:houseflies (3:7)
8*	0.8–1.2	56	84	126	*D. virilis*:houseflies (2:8)
9* and subsequent	0.9–1.4	56	84	126	*D. virilis*:houseflies (1:9)

removing spiders from their webs (Higgins 1992a). In addition to measuring the spiders using Helios ® needle-nosed calipers (TPL and abdomen length and abdomen width), we retrieved the shed exoskeleton, which served as a physical record of TPL of the prior instar. From abdomen length and width, we calculated abdominal volume as a cylinder and then used this volume and TPL to estimate spider mass after each molt [Higgins 1992a: mass (mg) = 12 + 81 (TPL cm^3) + 784 (abdomen volume cc)]. The size of hard portions of the exoskeleton does not change between molts and serves as a measure of size at each instar.

Weekly food availability (number of prey) was calculated based upon the mean mass of each prey type: *D. melanogaster* (mean mass 0.748 mg, SD = 0.110, n = 11), *D. virilis* (mean mass 1.60 mg, SD = 0.239, n = 15). Since the addition of high-protein dog-food to fly media increases the protein content of the prey and the survival of the spiders (Mayntz et al. 2003), all prey except *D. virilis* were reared on protein-supplemented diets. (*D. virilis* cultures grow slowly, and the addition of dog food to the media resulted in a high frequency of mold overgrowth, killing the culture.) At the seventh instar, we added commercially reared high-protein house flies to the diets (*Musca domestica*, SpiderPharm Inc; mean mass = 11.65 mg, SD = 2.077, n = 10). The qualitative shifts were necessary for logistical reasons. If we had fed only *D. melanogaster* through the entire development, the number of flies provided in later instars would have numbered in the hundreds per week due to the large size of the juvenile females. Within an instar, diet varied quantitatively, but not qualitatively, across treatment groups (Table 2).

Laboratory versus field growth.—In addition to testing for a priori effects of diet and family on juvenile developmental trajectories in the laboratory, we also tested whether juvenile growth in the laboratory was statistically distinct from juvenile growth in the field. Published records of growth per molt and intermolt duration serve as benchmarks (Higgins 1992a, 1993). Because the source populations for this laboratory experiment are not identical to those studied in the field, we took the mean slope of the growth per molt (Higgins 1993: Table 3) as the benchmark. The Mexican field studies did not include measurement of intermolt duration, but prior studies produced no detectable differences among sites as different as Texas and Panama, so we used regression of intermolt duration against spider size Higgins (1992a: Fig. 2) as the benchmark for intermolt duration for the laboratory.

We calculated an expected value of size as a function of premolt size and intermolt duration as a function of current spider size. We calculated expected spider size as $TPL_{postmolt}$ = 0.0567 + 1.263* $TPL_{premolt}$. We calculated expected instar duration as days intermolt = 7.18 + 8.56 (TPL). We then subtracted the expected from the observed and examined the distribution of the residuals as functions of family, diet, and instar.

Field censuses of prey capture.—In 1989–1990, LH worked in seven Mexican sites, including two of the sites from which these spiders were collected (Higgins 2000): Nanciyaga and Fortín de las Flores. The field studies included trap-line censuses of prey-capture success (Higgins & Buskirk 1992; Higgins 1993). The published analyses consider only median prey size and mean prey capture rates. To describe the foraging success of spiders in nature more fully, we here present an analysis of size distribution of prey, total prey mass captured as a function of spider size, and the likelihood of capture of different amounts of prey by spiders larger than TPL = 0.5 cm across all seven populations.

Size, age and instar at sexual maturity.—Female *N. clavipes* have heavily sclerotized epigynal plates allowing us to recognize when an individual molted to sexual maturity. We compared age, size, and instar at sexual maturity across all mature females on all diets to test for significant variation due to family. We compared across diets to test whether spiders with reduced diets take longer in each instar and therefore mature at a greater age (in days) but earlier instar (smaller size) relative to those on higher diets, thus avoiding end-of-season penalties detected in prior field studies (Higgins 2000).

Statistical analyses.—All statistical analyses were done in JMP (Version 7.0.2). Preliminary analyses of the distribution of age (time since initiation of treatment), instar duration and size (TPL) indicated that natural log transformation was necessary for normal distribution of developmental data; size

Table 3.—ANOVAs of female size and age at the ninth instar (log transformed).

	Source	*df*	SS	*F*	*P*
Size (ln TPL)					
	family	5	0.1478	2.6543	0.030
	diet	2	0.5960	26.76	< 0.0001
	family * diet	10	0.2376	2.133	0.033
	error	70	0.7797		
Age (ln days)					
	family	5	0.4158	5.223	0.0004
	diet	2	1.686	52.96	< 0.0001
	family * diet	10	0.3180	1.997	0.0465
	error	70	1.1144		

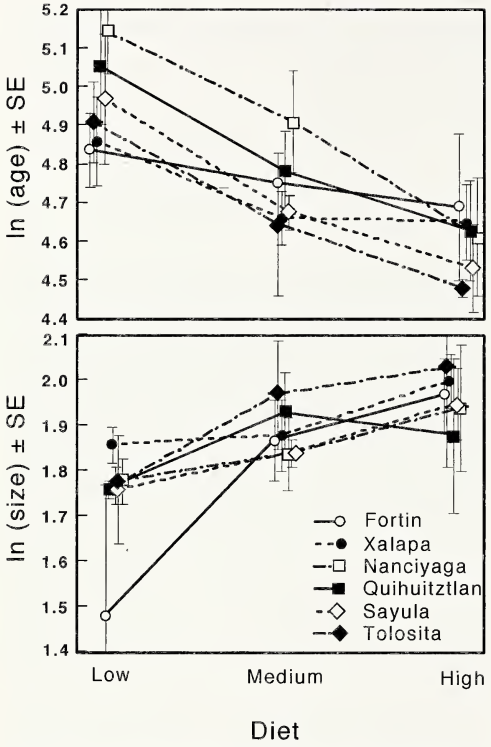


Figure 1.—Norm of reaction response to diet by age (days) and size (TPL) at which females reach the ninth instar (six instars of experimental treatment). Fortín females are significantly different from the other populations, driving a significant population x diet interaction.

data were transformed to mm prior to log-transformation. However, in the comparison of field and laboratory data, we found that the residuals of observed minus expected were normally distributed and hence required no transformation.

RESULTS

Developmental response to diet.—A total of 190 spiders molted to the fourth instar, and most spiders survived to the ninth instar (at which time all but three males had reached sexual maturity), allowing us to test for diet effects on development in known females (discarding data from individuals that died prior to the eighth instar). The diets significantly altered developmental trajectories of older juvenile females.

If, as we suspect, juvenile females are accelerating their growth rates in later instars to both reduce developmental asynchrony with males and to reduce risk of maturing late relative to the end of the season (Higgins 2000), we expected to find that spiders on low diets sacrifice growth per molt to pass through instars more quickly or to shorten their development by reducing the number of juvenile instars. We tested these predictions separately.

To test for cumulative changes in intermolt duration and growth per molt among spiders reared on different diets, we ran a MANOVA (multivariate analysis of variance) testing developmental differences in age and size at the ninth instar with diet and family as independent variables. We ran this analysis using data from spiders in the ninth instar (six experimental instars) because of high female mortality on low and medium food levels after this stage and because at this stage all males were identified and could be excluded. A total of 88 females reached the ninth instar. The fully-factoral MANOVA of ln (TPL) and ln (total time to ninth instar) was highly significant for both factors and the interaction (Fig. 3, whole model: Roy's Maximum Root (RMR) = 3.53, approximate $F = 14.51$, $df = 17$, $P < 0.001$; family: RMR = 0.458, $df = 5$, $P < 0.001$; diet: RMR = 2.752, $df = 2$, $P < 0.001$; family * diet: RMR = 0.353, $df = 10$, $P = 0.0134$).

Spiders on lower diets were smaller and reached the ninth instar later than spiders on the high diets. Examination of the E and H matrices showed that spiders from some families took longer to reach the ninth instar and were smaller when they did. Most interestingly, the interaction of family and diet reflects the fact that spiders from families that took less time to reach the ninth instar were more uniform in size across diets. Examination of the norm-of-reaction curves for each developmental parameter across all families (ANOVA, Table 3) shows that Fortín responded to diet with less change in time and great difference in size at the ninth instar (Fig. 1), and spiders from this family are presumably responsible for the significant interaction effects. We emphasize that because we only used one egg sac per family, we cannot know whether the unique developmental response by Fortín females represents a general characteristic of this population, or instead occurred because the particular family from Fortín was unusual.

The analysis of females at one single instar obscures changes that may take place as the spiders develop. To test for differences among families in the developmental responses to diet, we ran separate fully factorial ANCOVA with instar number (developmental stage) as the covariate, testing for developmental changes in instar duration and growth in TPL at each molt. As discussed in depth elsewhere (L. Higgins & C. Goodnight in prep.), we recognize that these analyses violate the assumption of independence of measures, since instar should be treated as a nested factor within individual. However, if instar is nested within individual, we cannot test for developmental effects of family and diet (detected as interaction between instar and the factor of interest), because each individual has only one family and diet assignment. Repeated measures ANOVA is also not permitted because developmental data are serially correlated, as demonstrated by the significant effect of instar number, and this violates the assumption of equal correlations between all pairs of observations. We therefore use instar as an independent cofactor as a compromise analysis.

Instar duration increases in later instars and is generally longer in spiders fed lower diets (Fig. 3). However, families varied significantly in their response to diet (family*diet) and in the rate at which instar duration increased (family*instar) (Table 4a). The rate of increase in instar duration was reduced

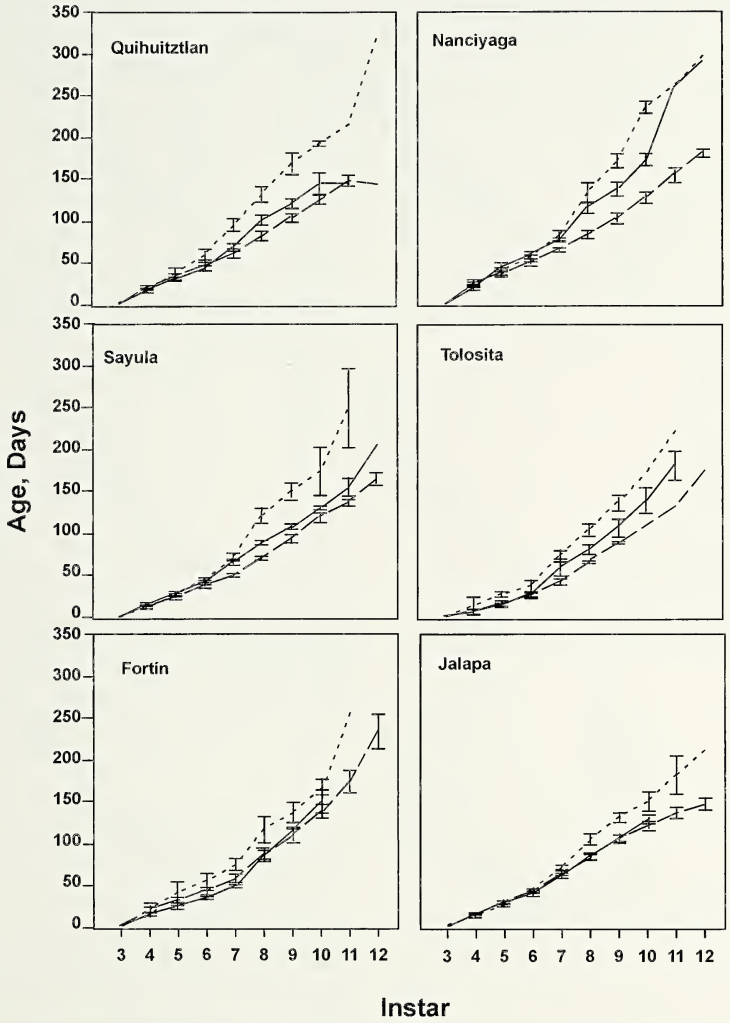


Figure 2.—Mean age (days, ± SE) of females at the molt to each instar, by diet (long dash: high; solid line: medium; short dash: low). Absence of error bar indicates a single surviving individual.

in well-fed spiders: spiders on low diets showed the greatest increase in instar duration as they passed through successive instars (diet*instar in Table 4a). The families did not differ significantly in how instar duration interacted with diet over the developmental trajectory (insignificant three-way interaction). To better understand how instar duration changes over development within each family, we present the regression equation for each family–diet combination in Table 5.

Figure 3 shows that these females increased in size with successive molts on all diets (compared to some arthropods where reduced diets result in molts without growth or even negative growth: Higgins and Rankin 1996). Compared to instar duration, the change in size at each molt responded less to the different experimental variables (Table 4b). Over all families, the change in TPL at each molt [calculated as ln (premolt TPL - postmolt TPL, cm)] increased slightly but

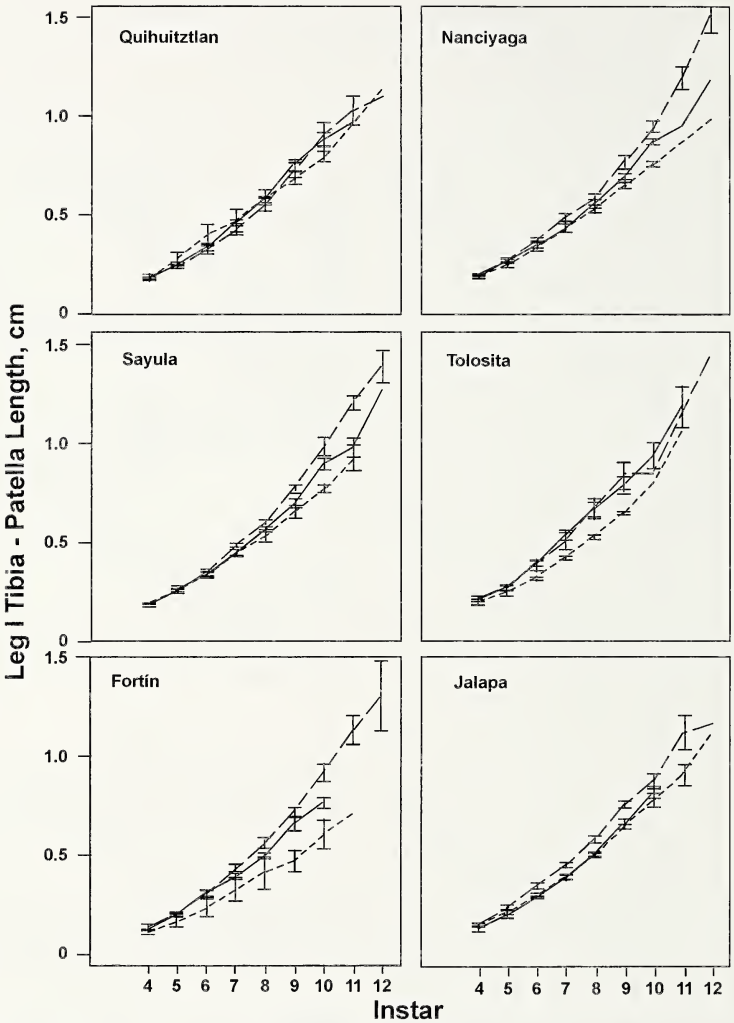


Figure 3.—Mean size (TPL, cm, ± SE) of females in each instar, by diet (long dash: high; solid line: medium; short dash: low). Absence of error bar indicates a single surviving individual.

significantly with successive molts. The rate of increase was unaffected by diet (no instar * diet effects). The significant effect of diet reflects differences in the intercept of the regression lines. Across all instars, diets, and families, growth per molt averaged 0.126 cm (n = 584 molts, SD = 0.062).

Growth in the laboratory versus in the field.—Extensive field data exist that describe growth of *N. clavipes* in Panama, various populations in Mexico, and Texas (Higgins 1992a, 1993). We used these observations to test whether the laboratory conditions produced normal development. ANCOVA showed that spiders were smaller at each instar compared to the field, and this difference increased as spiders grew (significant effect of instar: Table 6a). The deviation from field observations was less in the spiders fed high diets than those fed medium or low diets [diet effect: Student's t-test of LS mean differences = 1.96, P = 0.05; mean (SE)

Table 4.—ANCOVA of development across instars as a function of family and diet.

a. Instar duration (days, log transformed).

Source	*df*	SS	*F*	*P*
family	5	1.015	1.392	0.225
diet	2	16.01	54.92	< 0.0001
family*diet	10	3.021	2.072	0.0250
instar	1	51.09	350.5	< 0.0001
family*instar	5	3.411	4.680	0.0003
diet*instar	2	0.908	3.114	0.045
family*diet*instar	10	2.231	1.530	0.125
error	553	80.61		

b. Change in size at each molt (log transformed)

Source	*df*	SS	*F*	*P*
family	5	1.238	1.82	0.107
diet	2	7.652	28.16	< 0.0001
family*diet	10	1.553	1.143	0.327
instar	1	40.11	295.3	< 0.0001
family*instar	5	0.203	0.3000	0.9137
diet*instar	2	0.764	2.811	0.061
family*diet*instar	10	1.272	0.936	0.500
error	546	74.17		

deviations: high diet = −0.034 (0.003); medium diet = −0.0397 (0.0035); low diet = −0.0469 (0.0040)], but was unaffected by family. The three-way significant interaction of family, diet, and instar reflects that the Fortín spiders fed on low diets deviated more from the field observations than the other families. Similar ANCOVA analysis showed that the duration of each instar was longer in the laboratory compared to the field, the deviation increased as the spiders grew, and was affected by family and diet in complex fashion: all interactions except the three-way interaction were significant (Table 6b).

Table 5.—Instar duration increases in later instars (log transformed days between molts). * $P \leq 0.05$; ** $P < 0.01$ *** $P < 0.001$.

Family/ location	Diet	Intercept	Slope	R^2	*F* (*df*)
Fortín	High	2.095	0.215	0.658	78.97*** (1, 41)
	Med	1.858	0.307	0.646	27.31*** (1, 15)
	Low	2.469	0.165	0.227	4.984* (1, 17)
Xalapa	High	2.667	0.050	0.095	5.142* (1, 49)
	Med	2.393	0.138	0.424	16.21*** (1, 22)
	Low	2.557	0.159	0.426	24.44*** (1, 33)
Nanciyaga	High	2.192	0.158	0.468	50.183*** (1,57)
	Med	2.681	0.131	0.258	8.351 ** (1, 24)
	Low	2.504	0.228	0.525	34.78*** (1, 29)
Quihuitztlan	High	2.402	0.108	0.253	16.90*** (1, 50)
	Med	2.523	0.120	0.240	8.818** (1, 28)
	Low	2.875	0.129	0.233	5.165* (1, 17)
Sayala	High	2.295	0.131	0.391	35.91*** (1, 56)
	Med	2.513	0.114	0.421	21.80*** (1, 30)
	Low	2.391	0.260	0.550	43.93*** (1, 36)
Tolosita	High	1.955	0.223	0.672	30.72*** (1, 15)
	Med	2.119	0.233	0.519	25.85*** (1, 24)
	Low	2.228	0.266	0.592	14.53** (1, 10)

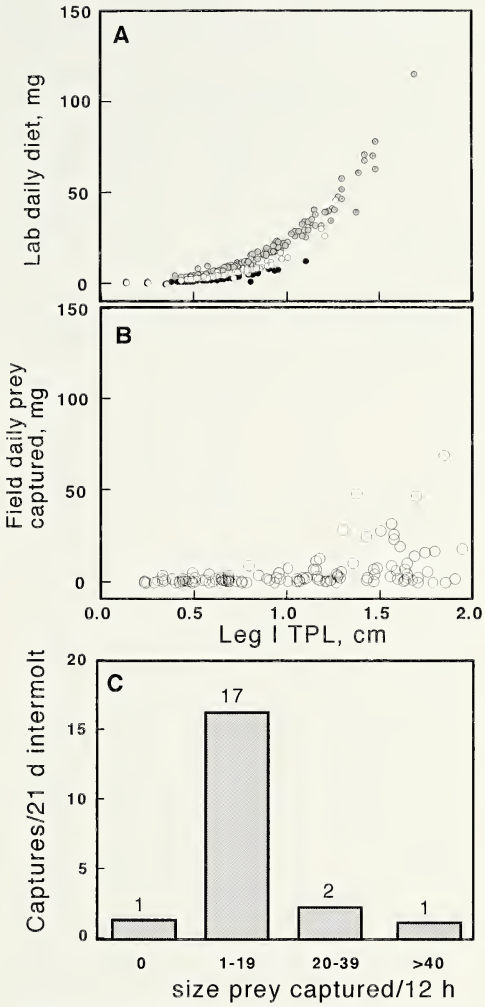


Figure 4.—Total daily prey (A) offered in the laboratory (black – low, white – medium, grey – high) and (B) captured in the field as a function of spider size. (C) For spiders of TPL ≥ 1.0 cm, there is low frequency of capture of large prey in each 21-day instar.

Size and age at sexual maturity.—Since instar duration responded more than growth per molt to diet and family effects, we expected that diet and possibly family would have significant effects on the total number of instars and thus on final size at maturity. Slowly growing spiders on lower diets would curtail their development at an earlier instar. However, we cannot test for family effects because only 25 females

Table 6.—ANCOVA comparisons of residuals of field versus laboratory growth, as measured by a) size and b) duration of *Nephila* instars.

a) Size at each instar as a function of instar number

Source	*df*	SS	*F*	*P*
family	5	0.00545	0.6033	0.697
diet	2	0.0234	6.471	0.002
family*diet	10	0.00827	0.4583	0.9167
instar	1	0.1532	84.86	< 0.0001
family*instar	5	0.00391	0.4339	0.8250
diet*instar	2	0.00507	1.406	0.2459
family*diet*instar	10	0.03665	2.030	0.0286
error	539	0.973		

b) Duration of each instar as a function of instar number.

Source	*df*	SS	*F*	*P*
family	5	0.6167	2.288	0.0451
diet	2	6.328	58.69	< 0.0001
family*diet	10	1.317	2.443	0.0076
instar	1	5.256	97.49	< 0.0001
family*instar	5	1.096	4.066	0.0013
diet*instar	2	0.4279	3.968	0.0196
family*diet*instar	10	0.3897	0.7227	0.703
error	456	24.59		

reached sexual maturity. Survivors are distributed across all family groups. Survival of high-diet individuals would have been greater but the humidifier in the walk-in chamber ceased running for nearly a week, and the resultant low humidity resulted in 75% mortality of the high-diet Xalapa females and nearly 40% mortality of the high- and medium-diet Quihuitzlan females. Interestingly, most of the small juveniles on low diets in the room survived, suggesting that low humidity, like low food availability, may have a disproportional impact on large juvenile females. With few individuals from each family and only slight developmental differences among families (none in growth/molt), we pooled across family to test for effects of diet on the size and age at maturity.

Both size and age at maturity were significantly altered by diet (MANOVA of log-transformed TPL and age (days since initiation of experiment); Roy's Maximum Root =1.808, approximate $F_{(2, 22)} = 19.89$, $P < 0.001$). A posteriori contrast determined that there was no significant effect of diet in the comparison of spiders fed high or medium food levels. Separate ANOVA confirmed that spiders fed high or medium diets matured significantly earlier ($F_{(2, 22)} = 9.29$, $P = 0.001$) and at a larger size ($F_{(2, 24)} = 7.18$, $P = 0.004$) (Table 7). At least within the limitations of this small sample, the number of juvenile instars was not determined by juvenile diet (ANOVA: $F_{(2, 22)} = 0.185$, $P = 0.83$; a power test shows 8% chance of failure to detect a significant difference). Thus, size variation among dietary groups must be due to the cumulative effects of differences in growth at each molt. Individuals reached sexual maturity in either the 11th or 12th instar, and both developmental pathways were represented in all three diet treatments (a non-independent test for effect of instar number on size at maturity showed no significant difference: $F_{(1, 23)} = 1.3$, $P > 0.3$). Importantly, the size of these mature females falls within but at the lower end of the range observed in the field in Mexico (Higgins 2000).

Realism of diet levels.—Compared to spiders observed in the field, those in the laboratory had longer intermolts, lower growth per molt, and smaller size at maturity. Together, these data suggest that even the high laboratory diets may be lower than the field. However, comparison to the field shows this is not the case. Comparing the mass of prey offered in the laboratory to observations from Mexican field studies, we found that the three feeding regimes for spiders smaller than 0.7 cm TPL were within the range of daily prey capture observed in the field, and the low and medium diets stayed within that range over all sizes of spider (Fig. 4A, B). The highest feeding regime was actually higher than most field observations for larger juveniles.

However, in the field, spiders capturing large masses of prey in a single day (> 50 mg: Fig. 4B) have captured rare, large prey items rather than many small items. Using the field data, we estimated the per-instar likelihood of capture of prey of different sizes using the average instar duration of large juvenile females in the field (21 days; Higgins 1992a). On average, a large juvenile female will only have a 50% chance of capturing one large insect during each instar (Fig. 2C) – in half of the larger instars, spiders fail to capture even one large insect. There is a 1.6% chance that any given spider will fail to capture any prey item larger than 10 mg in any given 21-day instar.

DISCUSSION

Developmental responses to differences in food quality, foraging success, and climate are ubiquitous and diverse among arthropods (reviewed in West-Eberhard 2003). *Nephila clavipes* females reared in the laboratory showed strong developmental responses to juvenile diets experienced, but contrary to our expectations, these responses did not include changes in the number of juvenile instars. Importantly, the size at maturity among these laboratory-reared spiders falls at the lower end of the range observed in the field. We propose that our high dietary treatment is actually the minimum at which females can reach sexual maturity, and that these needs are met in the field by the rare capture of very large insects.

As described by Higgins & Rankin (1996), arthropod post-embryonic development can be described by three parameters: intermolt duration, growth per molt, and number of juvenile instars. Combined with prior field data, our results suggest that in *N. clavipes*, these developmental parameters differ in their plasticity and respond to different aspects of prey capture.

Table 7.—Female size, instar, and age at sexual maturity in each diet group, pooled across families.

Diet	*n*	Mean TPL, cm (SD)	Mean age, days (SD)	Mean instar (SD)
High	18	1.29 (0.1623)	177.6 (29.22)	11.6 (0.502)
Medium	2	1.23 (0.0424)	204 (–)	11.5 (0.707)
Low	4	1.020 (0.0753)	259.3 (53.18)	11.8 (0.500)

Intermolt duration is far more variable than growth per molt in the field and in the laboratory. The experimental data we report here support previous hypotheses concerning the interrelationships between growth per molt and instar duration. Because change in size at each molt is closely correlated with premolt mass (Higgins 1992a), and growth per molt is relatively inflexible (see below and Higgins 1992a, 1993), Higgins (1992a) hypothesized that spiders with low prey-capture success experienced extended intermolt duration as they "waited" to accumulate necessary body mass for the next molt.

We did detect significant effects of diet on growth per molt; the spiders fed the lowest diets in the laboratory did show reduced growth per molt in each instar. In the laboratory, the lowest prey capture rates were at the low end of mean prey capture observed in the field. We suspect that spiders capturing such low amounts of food in the field fail to survive because of increased exposure to predators. Predation is very high on small and medium-sized juveniles (Higgins 1992b), and extending the intermolt period extends this period of vulnerability. Only in the laboratory could we observe plasticity in this developmental parameter. Such plasticity may be considered nonadaptive (sensu Ghalambor et al. 2007) in that it is a physiological response to environmental stress rather than an adaptive response to environmental variation.

As growth per molt varies little in field populations of *N. clavipes* (Higgins 1992a, 1993), the large amounts of variation in adult female size are necessarily due to differences in instar number (Higgins & Rankin 1996). However, we were unable to elicit variation in instar number in this experiment. Therefore, the observed variation in size at maturity among females fed different amounts of prey reflects accumulated differences in the growth per molt. Importantly, maturing females were at the low end of the range of sizes observed in the field. The laboratory mean female TPL of 1.2 cm is roughly one instar smaller than the mean of 1.8 cm TPL and two instars smaller than the largest spiders observed in the lowland tropical populations in Mexico (Higgins 2000). In contrast, males in this experiment matured at sizes that span the range observed in the field (L. Higgins & C. Goodnight pers. obs.). This is consistent with the idea that the variation in female size observed in the field reflects variation not in the baseline prey capture rates experienced by each individual (which is equivalent to food quantities in the laboratory), but rather variation in the rare capture of large insects.

We recognize that very few females reached sexual maturity in the laboratory: only 28% of the spiders that reached the ninth instar successfully matured, reflecting very high mortality in late instars on the low and medium diets (L. Higgins & C. Goodnight pers. obs.). We do not believe that this mortality reflects a qualitative nutritional deficit for several reasons. First, the diets we used fall within the range of mean prey-capture rates observed among the diverse Mexican populations (Higgins 2000) and match the feeding regimes that result in normal intermolt durations for small juveniles (Higgins & Rankin 2001). Second, protein-enhanced flies have been used successfully to rear a wide range of spiders including orb-weavers (e.g., Mayntz et al. 2003; G.W. Uetz pers. com.; C. Kristensen pers. com.) and male *N. clavipes* (L. Higgins & C. Goodnight pers. obs.). We have no reason to believe that juvenile *N. clavipes* females have distinct nutritional requirements from other orb weavers or from males of their own species.

We propose that although our laboratory diets fall within the range of observed mean prey-capture rates, they fail to mimic a different kind of variation, the rare capture of large insects (Venner & Casas 2005). Reanalysis of prior field data shows that capture of large insects is more irregular than previously appreciated. In addition to the mean biomass of prey (reported in Higgins 2000), larger juvenile and mature female spiders have a 50% chance of capturing one exceedingly large prey item per instar. We postulate that the capture of rare large prey is vital for successful female maturation in this species. Thus, variation in adult female size, determined primarily by variation in instar number, reflects variation in the rate of capture of large insects rather than simply variation in mean prey capture rate. As pointed out by Blackledge (2011), this may be a general phenomenon of orb-weaving spiders and requires a different approach to field and laboratory investigations of foraging and diet-dependent development and reproduction.

Based upon this hypothesis, we predict that the largest females in each population are adding juvenile instars (Esperk et al. 2007) and reaching large size because they inhabit good microhabitats, defined as those with high frequency of rare, large insects. Although diet-dependent variation in number of instars has been seen in other spiders [e.g., Mayntz et al. 2003 in the orb-weaver *Zygiella x-notata* (Clerck 1757)], it is by no means universal [e.g., Jespersen & Toft 2003 in the wolf spider *Pardosa prativaga* (L. Koch 1870)]. Some spiders, particularly smaller species, may have canalized their number of juvenile instars (e.g., Uhl et al. 2004). It is noteworthy that none of these species achieve size or mass approaching that of mature female *Nephila*, and that the numbers of juvenile instars are roughly half of that observed for females in the current study.

It has been proposed that most arthropod predators experience food limitation most of the time (Ward & Lubin 1993; Bilde & Toft 1998; Kreiter & Wise 2001). However, these studies involved much smaller species and emphasized female fecundity and the likelihood of reproduction rather than juvenile survival and development. Moreover, in most cases, the females were required to capture only a single large prey in order to reproduce successfully. The increasingly strong response to diet with higher instar number found in the current study may reflect the increasing metabolic needs of these giant females, particularly in populations with short time horizons relative to the total developmental time. An analogous dependence on rare, large prey has been found for penultimate and adult females of other spiders with female gigantism (LeGrand & Morse 2000; Moya-Laraño et al. 2003; Venner & Casas 2005). The fecundity advantage of female gigantism thus may come at the cost of increasing dependence upon repeated success at achieving a rare event, the regular capture of very large prey.

ACKNOWLEDGMENTS

This work would not have been possible without the efforts of a large number of people. Juan Nuñez Farfan and Jesus Vargas (Universidad Nacional Autonoma de México) and Pablo Berea facilitated collecting in Mexico, which was done

by Laura Hill and Lauren Gauthier (permit FLO 0014). Spider rearing in Vermont was accomplished in large part through the efforts of undergraduate volunteers Ashley Couture, Ariel GallentBernstein*, Lauren Gauthier*, Jon Hulce, Donald Kraft, Laina Lomina, Brian Mulcahy, Ryan Ofsthun, Catherine Oliver, Cynthia Quell, Jeff Schles, Abby Strauss, Rachel Taylor, and Sarah Wanamaker* (* two or more years). The research was supported in part by NSF Grant No. 0233440 to LEH.

LITERATURE CITED

Berner, D. & W.U. Blanckenhorn. 2006. Grasshopper ontogeny in relation to time constraints: adaptive divergence and stasis. Journal of Animal Ecology 75:130–139.

Berner, D. & W.U. Blanckenhorn. 2007. An ontogenetic perspective on the relationship between age and size at maturity. Functional Ecology 21:505–512.

Bilde, T. & S. Toft. 1998. Quantifying food limitation of arthropod predators in the field. Oecologia 115:54–58.

Blackledge, T.A. 2011. Prey capture in orb weaving spiders: are we using the best metric? Journal of Arachnology 39:205–210.

Calabrese, J.M., L. Ries, S.F. Matter, D.M. Debinski, R.N. Auckland, J. Roland & W.F. Fagan. 2008. Reproductive asynchrony in natural butterfly populations and its consequences for female matelessness. Journal of Animal Ecology 77:746–756.

Darwin, C. 1871. The Descent of Man, and Selection in Relation to Sex. John Murray, London.

Esperk, T., T. Tammaru, S. Nylin & T. Teder. 2007. Achieving high sexual size dimorphism in insects: females add instars. Ecological Entomology 32:243–256.

Fernandez-Montraveta, C. & J. Moya-Larano. 2007. Sex-specific plasticity of growth and maturation size in a spider: implications for sexual size dimorphism. Journal of Evolutionary Biology 20:1689–1699.

Ghalambor, C.K., J.K. McKay, S.P. Carroll & D.N. Reznick. 2007. Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. Functional Ecology 21:394–407.

Higgins, L.E. 1989. Effect of insemination on the morphology of the internal female genitalia of the spider *Nephila clavipes* (Araneae, Araneidae). Annals of the Entomological Society of America 82:748–753.

Higgins, L.E. 1992a. Developmental plasticity and fecundity in the orb-weaving spider *Nephila clavipes*. Journal of Arachnology 20:94–106.

Higgins, L. 1992b. Developmental changes in the barrier web structure under different levels of predation risk in *Nephila clavipes* (Araneae: Tetragnathidae). Journal of Insect Behavior 5:635–655.

Higgins, L. 1993. Constraints and plasticity in the development of juvenile *Nephila clavipes* in Mexico. Journal of Arachnology 21:107–119.

Higgins, L. 2000. The interaction of season length and development time alters size at maturity. Oecologia 122:51–59.

Higgins, L. 2002. Female gigantism in a New Guinea population of the spider *Nephila maculata*. Oikos 99:377–385.

Higgins, L. & R.E. Buskirk. 1992. A trap-building predator exhibits different tactics for different aspects of foraging behaviour. Animal Behaviour 44:485–499.

Higgins, L. & C. Goodnight. 2010. *Nephila clavipes* females have accelerating dietary requirements. Journal of Arachnology 38:150–152.

Higgins, L.E. & M.A. Rankin. 1996. Different pathways in arthropod postembryonic development. Evolution 50:573–582.

Higgins, L.E. & M.A. Rankin. 2001. Mortality risk of rapid growth in the spider *Nephila clavipes*. Functional Ecology 15:24–28.

Jespersen, L.B. & S. Toft. 2003. Compensatory growth following early nutritional stress in the wolf spider *Pardosa prativaga*. Functional Ecology 17:737–746.

Kreiter, N. & D. Wise. 2001. Prey availability limits fecundity and influences the movement pattern of female fishing spiders. Oecologia 127:417–424.

Kuntner, M. & J.A. Coddington. 2009. Discovery of the largest orbweaving spider species: the evolution of gigantism in *Nephila*. PLoS ONE 4(10):e7516.

Kuntner, M., J.A. Coddington & G. Hormiga. 2008. Phylogeny of extant nephilid orb-weaving spiders (Araneae, Nephilidae): testing morphological and ethological homologies. Cladistics 24:147–217.

LeGrand, R.S. & D.H. Morse. 2000. Factors driving extreme sexual size dimorphism of a sit-and-wait predator under low density. Biological Journal of the Linnean Society 71:643–664.

Mayntz, D., S. Toft & F. Vollrath. 2003. Effects of prey quality and availability on the life history of a trap-building predator. Oikos 101:631–638.

Miyashita, T. 1986. Growth, egg-production, and population-density of the spider, *Nephila clavata* in relation to food conditions in the field. Researches on Population Ecology 28:135–149.

Moya-Laraño, J., J.M. Orta-Ocaña, J.A. Barrientos, C. Bach & D.H. Wise. 2003. Intriguing compensation by adult female spiders for food limitation experienced as juveniles. Oikos 101:539–548.

Roff, D. 2001. Life History Evolution. Sinauer Associates, Sunderland Massachusetts.

Uhl, G., S. Schmitt, M.A. Schafer & W. Blanckenhorn. 2004. Food and sex-specific growth strategies in a spider. Evolutionary Ecology Research 6:523–540.

Venner, S. & J. Casas. 2005. Spider webs designed for rare but life-saving catches. Proceedings of the Royal Society B-Biological Sciences 272:1587–1592.

Ward, D. & Y. Lubin. 1993. Habitat selection and the life history of a desert spider, *Stegodyphys lineatus* (Eresidae). Journal of Animal Ecology 62:353–363.

West-Eberhard, M.J. 2003. Developmental Plasticity and Evolution. Oxford University Press, New York.

Manuscript received 18 February 2011, revised 29 July 2011.

2011. The Journal of Arachnology 39:409–419

Description of a new *Eukoenenia* (Palpigradi: Eukoeneniidae) and *Metagonia* (Araneae: Pholcidae) from Brazilian caves, with notes on their ecological interactions

Rodrigo Lopes Ferreira[1], Maysa Fernanda V. R. Souza[1], Ewerton Ortiz Machado[2,3] and Antonio Domingos Brescovit[2]: [1]Laboratório de Ecologia Subterrânea, Setor de Zoologia, Departamento de Biologia, Universidade Federal de Lavras, Lavras, Minas Gerais. CEP 37200-000, Brazil. E-mail: drops@dbi.ufla.br; [2]Laboratório de Artrópodes, Instituto Butantan, Avenida Vital Brazil, 1500, 05503-900 Butantã, São Paulo, SP, Brazil; [3]Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, Brazil

Abstract. Palpigradi comprises the most poorly known order within the Arachnida; hence, information regarding their biology and behavior is quite scarce. We document an interaction between a palpigrade of the genus *Eukoenenia* being preyed upon by a spider of the genus *Metagonia* in the Gruta do Vale, a cave in the municipal district of Felipe Guerra (Rio Grande do Norte, Brazil). The entire prey recognition and capture process by the *Metagonia* is described in full detail. Both species involved, *Eukoenenia potiguar* n. sp. and *Metagonia potiguar* n. sp., are also described. *Metagonia potiguar* n. sp. is the first Brazilian cave-dwelling *Metagonia* to be described.

Keywords: Predation, taxonomy, morphology, Brazil, Neotropics

The order Palpigradi Thorell 1888 currently contains 85 species, among which 66 belong to the genus *Eukoenenia* Börner 1901 (Harvey 2003; Barranco & Harvey 2008; Christian 2009; Souza & Ferreira 2010). These arachnids occur in various parts of the world, inhabiting soil, litter, caves, and other endogenous environments (Condé 1996). The world distribution of the group has its geographical limits between 48°N and 40°S, most of the species being registered in Europe and Africa (Condé 1996; Mayoral & Barranco 2002). Currently only five species of Palpigradi are known from Brazil: *Eukoenenia roquetti* (Mello-Leitão & Arlé 1935) from Rio de Janeiro, *E. janetscheki* Condé 1993 from Amazonia, *E. maquinensis* Souza & Ferreira 2010 from Cordisburgo, Minas Gerais, *E. ferratilis* Souza & Ferreira 2011 from iron ore caves, Minas Gerais, and *E. spelunca* Souza & Ferreira 2011 from Vargem Alta, Espírito Santo.

The spider genus *Metagonia* Simon 1893 currently has 81 species widely distributed in South and Central America (Platnick 2010). Mexico represents the northern geographical limit, with a large number of species. In South America, there are 26 species, of which 13 species occur in Brazil. Most *Metagonia* species are leaf-dwelling, but some live in caves (Gertsch 1986; Gertsch & Peck 1992; Huber 1998), and a few are known from leaf litter habitats (Gertsch 1986; Huber et al. 2005). Some species have troglomorphic traits (Gertsch 1986; Huber 1998), and at least three species occur in cave environments as eyeless troglobites: *M. bellavista* Gertsch & Peck 1992 and *M. reederi* Gertsch & Peck 1992, both from the Galapagos Islands, and *M. debrasi* Pérez González & Huber (1999) from Cuba.

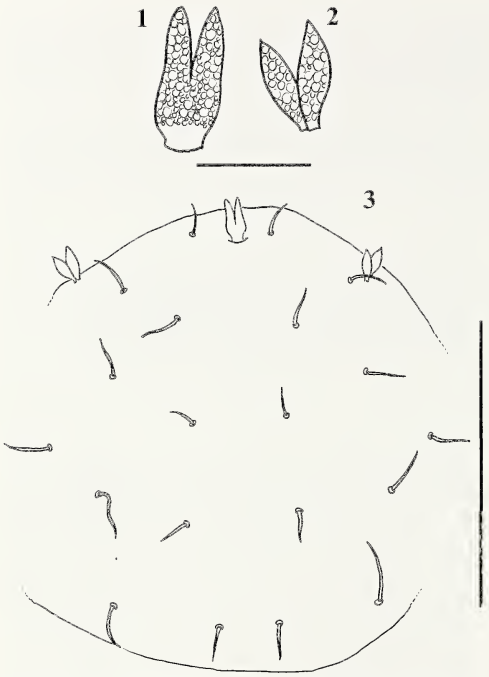
The biology of *Metagonia* species can be divided into three categories (some examples are given): leaf-dwellers, such as *M. rica* Gertsch 1986 (Gertsch 1986; Huber 1997), *M. maritaguariensis* González-Spoga 1998 (Huber 2004), *M. osa* Gertsch 1986 and *M. uvita* Huber 1997 (both in Huber & Schüte 2009); leaf litter dwellers, such as *M. paranapiacaba* Huber et al. 2005 and *M. petropolis* Huber et al. 2005 (Huber *et al.* 2005); and cave dwellers, such as *M. blanda* Gertsch 1973 (Huber 1998), *M. debrasi* Pérez González & Huber 1999 (González & Huber 1999).

Most of these papers provide general descriptions of the natural history of the species. However, Huber (1997) gives a good description of their biology, and Huber & Schüte (2009) present a complete study about their habitat preferences, web construction and prey. Little information exists on the prey consumed by some species of *Metagonia*. Furthermore, until now, documented reports of interaction of any species with individuals of the order Palpigradi have not existed, especially with respect to their potential predators. Therefore, the present work presents an account of the predation of an individual of the genus *Eukoenenia* by an individual of the genus *Metagonia* observed at the Gruta do Vale, located in the municipal district of Felipe Guerra (Rio Grande do Norte, Brazil). Both individuals, together with the other specimens of these genera found in the same cave, belong to new species that are described in the present work.

METHODS

We examined the specimens of *Eukoenenia* by clearing them in Nesbitt's solution and mounting them in Hoyer's medium on 3 × 1-inch (7.6 × 2.5 cm) glass slides using standard procedures for mites (Krantz & Walter 2009). All measurements are presented in micrometers (μm) and were taken using an ocular micrometer with a compound microscope. Body length was measured from the apex of the propeltidium to the posterior margin of the opisthosoma.

The following abbreviations were utilized, based on Barranco & Mayoral (2007): L = total body length (without flagellum), B = dorsal shield length, P = pedipalpus, I and IV = legs I and IV, ti = tibia, bta1 = basitarsus 1, bta2 = basitarsus 2, bta3 = basitarsus 3, bta4 = basitarsus 4, ta1 = tarsus 1, ta2 = tarsus 2, ta3 = tarsus 3, a = width of basitarsus IV at level of seta r, er = distance between base of basitarsus IV and insertion of seta r, grt = tergal seta length, gla = lateral seta length, r = stiff seta length, t/r = ratio between length of basitarsus IV and stiff seta length, t/er = ratio between basitarsus IV length and distance to insertion of stiff seta, gla/grt = ratio between lengths of lateral and tergal setae, B/bta = relation between lengths of prosomal shield and basitarsus IV,



Figures 1–3.—*Eukoenenia potiguar* new species, paratype male: 1. Frontal organ, dorsal view; 2. Lateral organ, dorsal view; 3. Propeltidial chaetotaxy. Scale bars 20 μm (Fig. 1), 20 μm (Fig. 2), 60 μm (Fig. 3).

bta/ti = ratio between lengths of basitarsus IV and tibia IV, FI–FVIII = flagellar segments. Setal nomenclature follows that of Condé (1989, 1993).

All morphological observations and illustrations of *Metagonia* were made using a Leica MZ12 stereomicroscope with camera lucida. The epigynum was dissected and immersed in clove oil for visualization of internal structures following Levi (1965). Descriptions and measurements follow Huber (2000). Measurements are given in millimeters. The ratio tibia I length/diameter (L/d) is a measure of the robustness of the legs (Huber 2000).

The material examined was deposited in the following institutions (abbreviation and curator in parentheses): Coleção de Invertebrados Subterrâneos de Lavras, Universidade Federal de Lavras (ISLA, R.L. Ferreira) and Coleção de Artrópodes e Miriápodes, Instituto Butantan, São Paulo (IBSP, I. Knysak).

RESULTS

TAXONOMY

Order Palpigradi Thorell 1888
Family Eukoeneniidae Petrunkevitch 1955
Genus *Eukoenenia* Börner 1901

Koenenia Grassi & Calandruccio 1885:165 [junior primary homonym of *Koenenia* Beushausen 1884 (Mollusca: Bivalvia)]. *Koenenia* (*Eukoenenia*) Börner 1901:551.

Type species.—*Koenenia mirabilis* Grassi & Calandruccio 1885, by monotypy.

Eukoenenia potiguar new species
(Figs. 1–19)

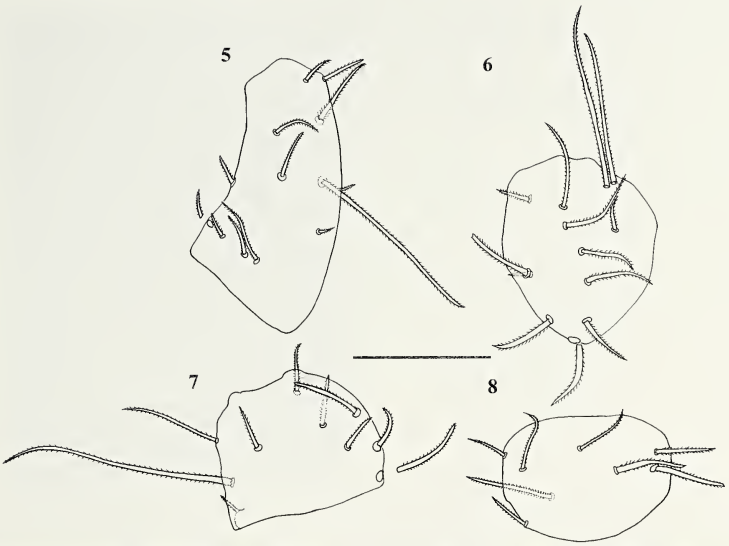
Types.—Holotype male ("male I"), "Gruta do Vale" (05°31′51″S, 37°36′58″W) Felipe Guerra, Rio Grande do Norte, Brazil, 18 July 2009, R. L. Ferreira (ISLA 1293). Paratypes: 1 male (ISLA 1294), 2 females (ISLA 1295, 1296), 1 juvenile female (ISLA 1297) and larva (ISLA 1298), collected with holotype; 1 female, "Gruta Boca de Peixe" (05°29′04.5″S, 37°33′29.6″W), Governador Dix Sept Rosado, Rio Grande do Norte, Brazil, 3 June 2010, D.M. Bento (ISLA 1299).

Additional material examined.—BRAZIL: *Rio Grande do Norte*: 1 ♀, Capoeira do João Carlos cave, Governador Dix Sept Rosado, 3 June 2010, D.M. Bento (IBSP 001); 1 larva, Gruta Crotes cave, 4 June 2010, D.M. Bento (IBSP 002).

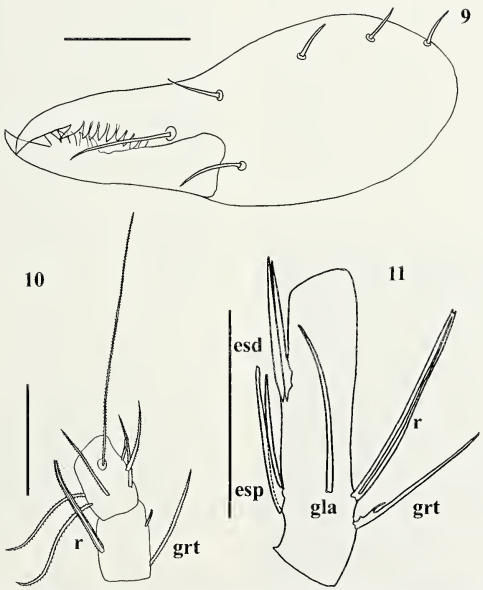
Etymology.—The new species is named *potiguar* in reference to those born in the State of Rio Grande do Norte, Brazil. The name is to be treated as a noun in apposition.

Diagnosis.—*Eukoenenia potiguar* differs from all other species of the genus by the following combination of traits: two blades in the prosomal lateral organs, tergite II with two pairs and a central seta (t, t_1, t_3,) between both slender setae (s), tergites III–VI with three pairs of setae (t', t_1, t_3) between both slender setae (s), sternites IV–VI with 2 + 2 thickened setae (a_1 and a_2) between two normal slender setae (s_1 and s_2),

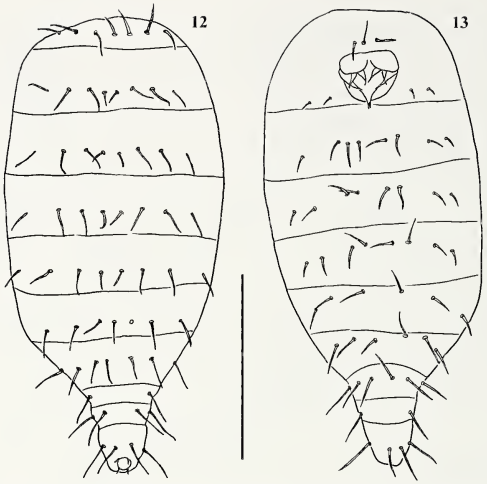
Figure 4.—*Eukoenenia potiguar* new species, paratype male: deuto-tritosternal setae. Scale bar 50 μm.



Figures 5–8.—*Eukoenenia potiguar* new species, holotype male: 5. Coxa I; 6. Coxa II; 7. Coxa III; 8. Coxa IV. Scale bar 60 μm.



Figures 9–11.—*Eukoenenia potiguar* new species, paratype male (Figs. 9, 10) and holotype male (Fig. 11): 9. Chelicerae; 10. Basitarsus 3–4 of leg I; 11. Basitarsus IV. Scale bar 60 μm.



Figures 12,13.—*Eukoenenia potiguar* new species, paratype male: 12. Opisthosoma, dorsal view; 13. Opisthosoma, ventral view. Scale bar 60 μm.

and the characteristic chaetotaxy and shape of the genitalia in females and males.

Description of adults.—*Prosoma:* frontal organ with 2 branches, pointed apically, each 4.5 times longer than wide (22.5 μm/5 μm) (Fig. 1). Lateral organ with 2 blades, each 4 times longer than wide (20 μm/5 μm) (Fig. 2). Propeltidium with 10 + 10 setae in 5 rows, outer pair on last row longer than others (Fig. 3). Metapeltidium with 3 + 3 setae (t_1, t_2, t_3), outer setae shortest (67 μm, 77 μm, 45 μm). Nine deuto-tritosternal setae in 2 rows: first with 3 setae in V arrangement and second with 6 setae in linear arrangement (Fig. 4). Male holotype with only 6 deuto-tritosternal setae.

Coxal chaetotaxy: males: coxa I with 13 setae (Fig. 5); coxa II with 3 thick and 10 normal setae (Fig. 6); coxa III with 3 thick and 7–9 normal setae (Fig. 7); coxa IV with 2 thick and 6 normal setae (Fig. 8). Females: coxa I with 15 setae; coxa II with 4 thick and 8 normal setae; coxa III with 3 thick and 8 normal setae; coxa IV with 2 thick and 8 normal setae.

Chelicerae: with 9 teeth on either finger; 4 dorsal setae and a single ventral seta inserted near third segment and single seta inserted near row of teeth of second segment (Fig. 9).

Legs: basitarsus 3 of leg I short, 1.5 times longer than wide, with 3 setae (*grt* 55 μm; *r* 52.5 μm). Seta r longer than segment (37.5 μm/52.5 μm, *tlr* = 0.7), inserted in proximal half and reaching distal margin of basitarsus 4 (32.5 μm/15 μm, s/er = 2.1) (Fig. 10). Basitarsus of leg IV 4.25 times longer than wide, with 7 setae (2 *esd*, 2 *esp*, *gla*, *grt* and *r*), bta/ti 0.8. Stiff seta r 1.44 times shorter than tergal edge of article (85 μm/62.5 μm,

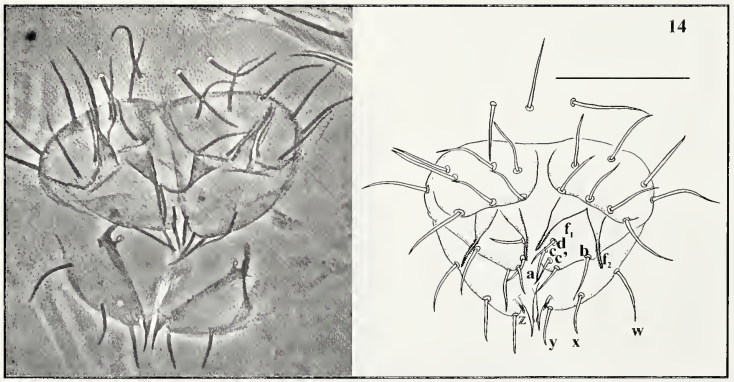


Figure 14.—*Eukoenenia potiguar* new species, holotype male (photograph) and paratype male (drawing): Male genitalia. Scale bar 60 μm.

Figure 15.—*Eukoenenia potiguar* new species, female II (paratype): female genitalia. Scale bar 60 μm.

tlr = 1.36) and inserted in proximal third (85 μm/30 μm, *tler* = 2.8). Setae *esp, grt* and *gla* in proximal half (Fig. 11).

Opisthosoma: tergite II with 3 + 1 + 3 dorsal setae, 2 pairs and a central seta (t_1, t_1, t_3) between both slender setae (*s*). Tergites III–VI with 4 + 4 setae, 3 pairs of setae (t', t_1, t_3) between both slender setae (*s*), central pair shortest (Fig. 12). Sternite III with 2 + 2 setae. Sternites IV–VI each with 2 + 2 (3 + 2 in the male paratype) thickened setae (a_1 and a_2) between 2 slender normal setae (s_1 and s_2) on each side (Fig. 13); a pair of glandular pores situated between a_1 setae. In one female, sternite IV only possesses one s seta and sternite VI possesses 1 more s seta (3 setae). Segments VII–XI showing some variation in the number of setae, with 13, 13–15, 8, 6–8 and 8–9 setae, respectively, in males, and with 14–15, 14–15, 8, 8 and 9–10 setae, respectively, in females.

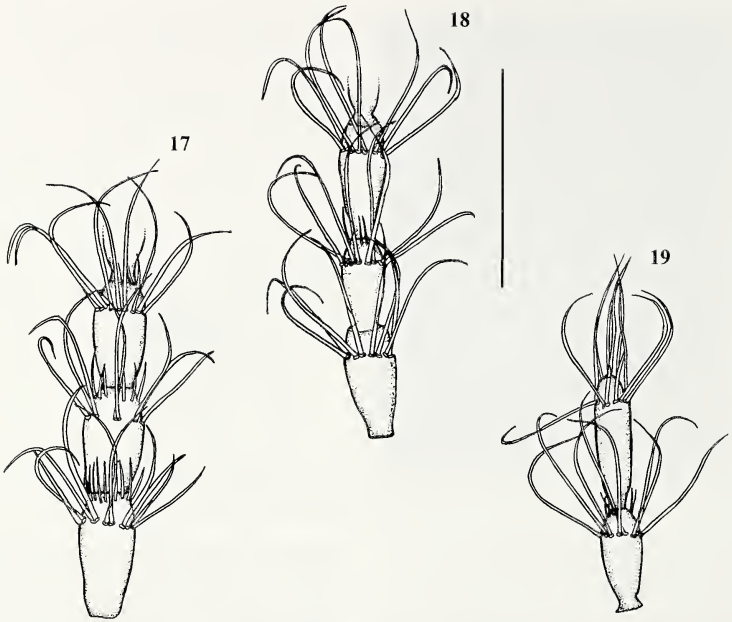
Male genitalia: with 2 + 2 sternal setae in holotype (one asymmetrically missing in male paratype). With 40 (38 in the male II) setae distributed in 3 lobes. First lobe broad and short; with a clear separation in central region, with 9 + 9 setae in 2 rows in male holotype, proximal row with 5 + 5 setae and distal row with 4 + 4. Male II has only 8 + 8 setae in 2 rows, each with 4+4 setae. In addition, 2 pairs of fusules on distal margin; fusules short, similar in length (f_1 = 25 μm; f_2 = 27.5 μm), conical, very close to each other. Second lobe subtriangular, with a rounded apex, with 5 + 5 setae (*a, b, c, c', d*). Third lobe also in a subtriangular form, well developed, with 4 + 4 setae (w, *x, y, z*), with a large, pointed and bifurcate, apical section. In each half of third lobe, two areas can be distinguished: a glabrous inner area, and an external area that possesses micro-setae (a pubescent area) (Fig. 14).

Female genitalia: with 2 lobes, first lobe with 10 + 11 setae (asymmetry caused by lack of regular setae): 2 + 2 sternal setae (st_1 and st_2) followed by 2 + 2, 1 + 2, 1 + 1 and 4 + 4 distal setae, of which a_1, a_2, a_3, a_4 measure 15 μm, 12.5 μm, 20 μm, and 21 μm respectively. Second lobe with 3 + 3 setae (x, y, z), measuring 31 μm, 17.5 μm, and 20 μm respectively; 4 glandular orifices (Fig. 15). Spermatheca shaped like an inverted "U," formed by 2 lobes linked at their base (Fig. 16).

Flagellum: with 8 segments in one juvenile specimen and 7 in an adult (the last flagellar segment is lacking). First segment with 9 long setae inserted in distal half. Second, third, fourth, fifth and sixth segments with 8 long setae inserted in distal half. Seventh segment with 6 long setae, respectively, inserted in distal half. Segments 1, 2, 3, 5 and 7 with an apical crown of spines.

Figure 16.—*Eukoenenia potiguar* new species, female III (paratype): spermatheca detail. Scale bar 20 μm.

Description of the immature stages.—*Juvenile female:* lateral organ with 2 blades. Deuto-tritosternum with 7 setae. Fingers of chelicera with 8 teeth. Chaetotaxy of propeltidium and metapeltidium complete. Tergites II–VI with 2 + 2 setae (t) between the setae s. Sternites IV–VI as in adult, except for absence of setae s_2; two gland orifices present. Segments VII–XI with 11, 12, 8, 8 and 8 setae. Primordia of genital lobes developed on segments II and III, but unfortunately it was not



Figures 17–19.—*Eukoenenia potiguar* new species, juvenile female: 17. Flagellar segments I, II and III; 18. Flagellar segments IV, V and VI; 19. Flagellar segments VII and VIII. Scale bar 60 μm.

possible to determine the number and position of the setae due to damage during slide mounting. Flagellum with 8 short segments (total length 597.5 μm). First 3 segments with 10, 8, and 9 long setae, respectively, inserted in distal half (Fig. 17). Fourth, fifth, sixth and seventh segments with 8 long setae inserted in distal half. Last segment longer than others, with 8 long setae inserted in distal half and 3 long setae inserted apically. Segments 1, 2, 3, 5 and 7 with an apical crown of spines. (Figs. 18, 19).

Larva, sex indeterminable: deuto-tritosternum with 3 setae. Chaetotaxy of propeltidium and metapeltidium complete. Coxae II–IV with 3, 3, and 0 thickened setae. Trichobothria and forked setae as in adult. Leg IV bta with setae (r and 2 esd). Tergites II–VI with 2 + 2 setae (t) between the setae s. Sternites IV–VI with setae a_1 and a_2, setae s missing. Sternite II with 2 + 2 sternal setae (st_1, st_2), sternite III with 3 + 3 (st_1, st_2, st_3).

Dimensions (μm)*:* See Table 1.

Remarks.—This species has the lateral organ formed by 2 blades, a characteristic present in only other two species of the genus *Eukoenenia*: *E. lienhardi* Condé 1989 from Sumatra (that can have 3, 2, or only 1 blade) and *E. singhi* Condé 1989 from India. *Eukoenenia lienhardi* and *E. singhi* are very similar species that share several characteristics with *E. potiguar*, such as the chaetotaxy of the opisthosomal tergites II–VI (also found in the African species *E. lawrencei* Rémy 1957), the presence of 2 + 2 setae between the two setae a in the opisthosomal sternites IV–VI, the number of setae in the basitarsus IV, and chelicerae with nine teeth. Furthermore, *E. potiguar* also shares the same number of setae in the deuto-tritosternum with *E. singhi*. However, these species can be clearly separated by the form of the genital lobes and the spermatheca of the females. It is not possible to make comparisons of the male genitalia because the two Asian species described were based only on female specimens (Condé 1989).

It is important to emphasize that the new species has quite different characteristics from those observed in the two Brazilian edaphomorphic species already described, clearly differing from *E. janetscheki* Condé 1993 (Amazonia) mainly in the chaetotaxy of the opisthosomal tergites, the number of lateral organs, the chaetotaxy, and the form of the male and female genital lobes; and from *E. roquetti* (Mello-Leitão & Arlé 1935) mainly in the number of elements that form the lateral organs and the form and chaetotaxy of the male genitalia (Mello-Leitão & Arlé 1935; Condé 1993, 1997).

The general aspect of the male genitalia of *E. potiguar* resembles that of *E. guzikae* Barranco & Harvey 2008 from Australia, in that both species have the first lobe short and wide, conical fusules, short and near each other and the second lobe with 5 pairs of setae. However, the male genitalia of *E. potiguar* differs from that of the male of *E. guzikae* mainly by having the first lobe clearly separated in two halves, the fusules without a median constriction, the second lobe with a rounded apex, and the third lobe with four pairs of setae.

Table 1.—Measurements (μm) of selected body parts of the seven type specimens of *Eukoenenia potiguar*.

Body part	Male I (Holotype)	Male II	Female I	Female II	Female III	Juvenile female	Larva
L	1085	1155	1225	1150	1220	1060	575
B	272.5	250	295	280	290	227.5	207.5
Pti	95	90	97.5	97.5	100	87.5	55
Pbta1	40	37.5	40	37.5	40	32.5	25
Pbta2	35	35	37.5	42.5	40	32.5	25
Pta1	25	30	30	50	30	25	22.5
Pta2	27.5	27.5	30	42.5	30	27.5	25
Pta3	50	45	47.5	40	52.5	42.5	40
Iti	-	110	110	110	117.5	-	65
Ibta1+2	85	87.5	85	90	87.5	82.5	55
Ibta3	37.5	37.5	40	42.5	42.5	32.5	22.5
Ibta4	40	37.5	35	45	45	32.5	25
Ita1	20	17.5	20	17.5	25	17.5	15
Ita2	30	27.5	27.5	30	32.5	25	20
Ita3	97.5	97.5	100	100	102.5	92.5	80
IVti	105	105	-	112.5	112.5	-	67.5
IVbta	85	77.5	-	102.5	92.5	-	55
IVta1	40	40	-	42.5	40	35	32.5
IVta2	50	55	-	60	52.5	45	45
A	20	20	-	20	25	-	15
Er	30	27.5	-	32.5	27.5	-	20
Grt	47.5	47.5	-	40	50	-	-
Gla	50	57.5	-	52.5	55	-	-
R	62.5	62.5	-	65	62.5	-	50
tlr	1.36	1.44	-	1.57	1.48	-	1.1
tler	2.83	3.27	-	3.1	3.36	-	2.75
gla/grt	1.05	1.21	-	1.3	1.1	-	-
B/btaIV	3.2	2.7	-	2.7	3.1	-	3.7
btaIV/tiIV	0.8	0.85	-	0.9	0.82	-	0.8
FI	-	-	-	77.5	-	80	-
FII	-	-	-	72.5	-	65	-
FIII	-	-	-	72.5	-	80	-
FIV	-	-	-	75	-	75	-
FV	-	-	-	55	-	62.5	-
FVI	-	-	-	72.5	-	75	-
FVII	-	-	-	52.5	-	72.5	-
FVIII	-	-	-	-	-	87.5	-

Although the specimens of *E. potiguar* have only been collected in caves, the species does not show any obvious specialization linked to the cave environment because the B/btaIV and btaIV/TiIV ratio values are within the range commonly found in endogeomorphic species according to Condé (1998). It is noteworthy, however, that the conditions outside these caves, within the domain of the Caatinga (the only Brazilian semi-arid biome), are extremely restrictive. Thus, it is believed that organisms of this species are unlikely to be found in epigean or endogenous surface systems throughout the whole year. However, in the few rainy months that occur in the area, such organisms may be found closer to the surface, but this claim is certainly speculative, and this question deserves to be the target of future studies.

Order Araneae Clerck 1757
Family Pholcidae Koch 1851
Genus *Metagonia* Simon 1893

Metagonia Simon 1893:472; Gertsch 1971:82–83; Gertsch 1977:105; Gertsch 1986: 40–41; Gertsch & Peck 1992:1194–1195; Huber 1997a:342.

Anomalaia González-Sponga 1998:24.

Type species.—*Metagonia: Metagonia bifida* Simon 1893, by original designation.

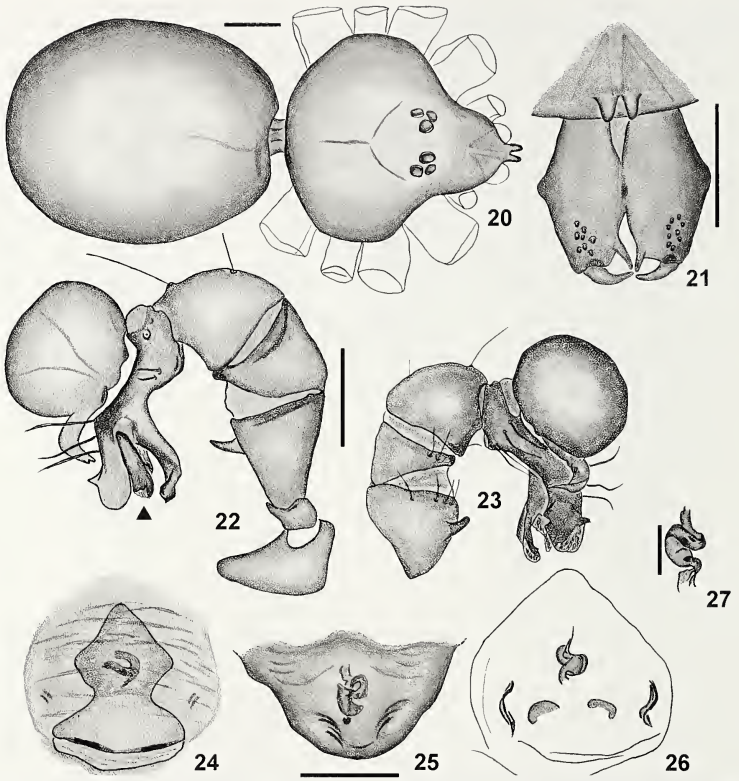
Anomalaia: Anomalaia mariguitarensis González-Sponga 1998, by original designation.

Metagonia potiguar new species
(Figs. 20–27)

Types.—Male holotype, "Gruta do Vale" (05°31′51″S, 37°36′58″W), Felipe Guerra, Rio Grande do Norte, Brazil, 18 July 2009, R.L. Ferreira (IBSP 145155). Paratype: 1 female, collected with holotype (IBSP 145156).

Etymology.—The new species is named *potiguar* in reference to those born in the State of Rio Grande do Norte, Brazil. The name is to be treated as a noun in apposition.

Diagnosis.—The male can be distinguished from other *Metagonia* species by the simple pair of clypeus apophyses (Figs. 20, 21), strong femoral dorsal apophysis, procursus shape with large hinged process and globular abdomen (Fig. 20). The female can be distinguished by the shape of her sclerotized ducts (Figs. 26, 27) and globular abdomen.



Figures 20–27.—*Metagonia potiguar* n. sp. (Holotype and paratype): 20. Male body, dorsal; 21. Male chelicerae, frontal; 22, 23. Male left palp; 22. Retrolateral (arrow indicates hinged process); 23. Prolateral, slightly ventral; 24–27. Female epigynum, 24. Ventral; 25. Anterior; 26. Dorsal; 27. Internal ducts. Scale bar 0.25 mm, except fig. 27: 0.10 mm.

Description.—*Male (holotype):* Total length 2.5, carapace length 0.8, width 0.8, leg I 17.4 (4.1 + 0.4 + 4.7 + 7.1 + 1.1), tibia II 3.1, tibia III missing, tibia IV 2.9; tibia I l/d 43. Body as in Fig. 20. Carapace pale yellow without stripes or spots (Fig. 20). Ocular area without color differentiation. Distance PME-ALE about 17% of PME diameter. Clypeus with a pair of small, simple, and straight apophyses (Figs. 20, 21). Sternum pale yellow. Chelicerae pale yellow, with club shaped hairs, without apophysis (Fig. 21). Palps (Figs. 22, 23) pale yellow, procursus ochre; femur with a pointed ventral apophysis; procursus split into a simple ventral projection with a twisted tip, a strong and simple dorsal projection, and a retrolateral hinged process (Fig. 22); bulb simple with a small embolus (Fig. 23). Legs yellowish, without spines, without modified hairs, retrolateral trichobothrium of tibia I at 12%, tarsus I with approximately 14 pseudosegments. Abdomen globular (Fig. 20), completely pale yellow, genital plate rectangular, light brown.

Female (paratype): Total length 2.2, carapace length 0.8, width 0.8, leg I 14.9 (3.7 + 0.4 + 4.0 + 5.7 + 1.1), tibia II 2.5, tibia III 1.8, tibia IV -. In general, very similar to male, without clypeus modification. Epigynum brown, approximately triangular with median lateral indentations (Fig. 24) and a central elevation bordered by two lateral excavations (Fig. 25). Internal genitalia with a pair of barely visible small pore fields (Fig. 26) and a system of asymmetrical, sclerotized, central ducts (Fig. 27).

Distribution.—This species is currently known only from the type locality.

Remarks.—*Metagonia potiguar* does not seem to fit convincingly within any of the five operational species-groups proposed by Huber (2000). However, it shows similarities to "group 1": sclerotized epigynum, ventral apophysis on the palpal femur, and bifid clypeus apophysis. The main difference lies in the globular abdomen, which is bifid in the majority of the "group 1" species. This trait could be due to habitat pressures, as stated in Huber *et al.* (2005). *Metagonia potiguar* represents the first record of *Metagonia* in Brazilian caves.

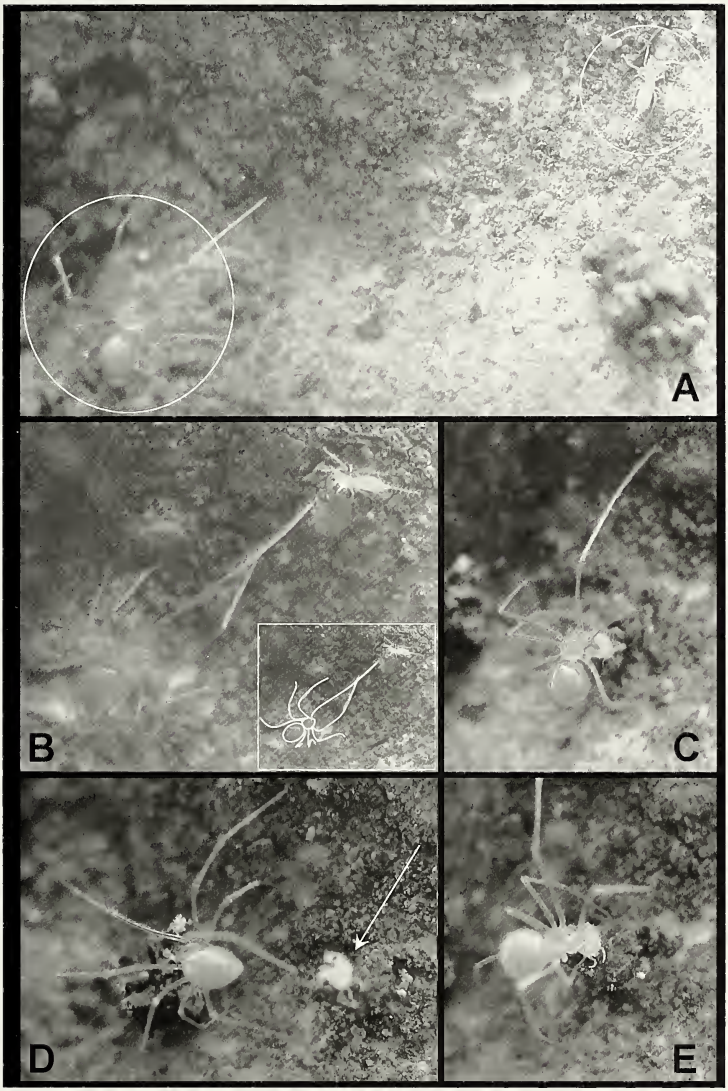


Figure 28.—Interaction repertoire: A. Individuals of *Metagonia potiguar* and *Eukoenenia potiguar* found when rock was overturned; B. *Metagonia* reaching *Eukoenenia* and touching it with a leg (in detail, white line indicating the *Metagonia*); C. *Metagonia* wrapping prey with some web filaments, holding it for some seconds, while prey struggles; D. Prey briefly abandoned; E. *Metagonia* returns and begins to feed.

DISCUSSION

Ecological interactions.—Individuals of both species, *Metagonia potiguar* and *Eukoenenia potiguar*, were under a rock fragment on the floor of the cave, in its more interior portion. The locality was aphotic. The rock, supported on earthy sediment, was located near a speleothem under a formation. The dripping made the surrounding environs more humid, including the sediment on which the rock rested. As soon as we overturned the rock, we observed the individuals. We settled the rock again on the floor, leaving the organisms visible.

When the rock was overturned, *Metagonia* remained immobile while *Eukoenenia* began moving, continually changing direction, always groping with the first pair of legs, maintaining the flagellum erect and perpendicular to the substrate, making lateral movements. *Eukoenenia* progressively began to approach *Metagonia*, until when about a centimeter away, *Metagonia* noticed its presence. Apparently *Eukoenenia* bumped into a thread of *Metagonia* web because it immediately changed position and began moving in the opposite direction from *Metagonia*, maintaining the "random" change of direction behavior (Fig. 28A). *Metagonia*, in turn, began moving towards *Eukoenenia*, feeling with the first pair of legs. When it finally reached *Eukoenenia* and touched it with one of its legs (Fig. 28B), it immediately jumped on *Eukoenenia*, grasping it with its chelicerae (Fig. 28C). *Metagonia* quickly wrapped the prey with some web filaments, maintaining its hold for several seconds, while the prey struggled. After immobilizing the prey, it briefly abandoned *Eukoenenia* (Fig. 28D), but after about 10 seconds, returned and began to feed (Fig. 28E). At that moment, the process was interrupted by the collection of both individuals.

Although a certain amount of attention has been drawn to the order Palpigradi in recent years (e.g., Barranco & Harvey 2008; Král et al. 2008; Christian 2009; Pepato et al. 2010), practically nothing is known of the ecological relationships exhibited by these organisms. Information regarding feeding habits, prey, predators, and more has been, until now, unknown, which makes the group even more enigmatic. The few references about possible interactions registered in the literature are almost totally speculative. This work represents the first description of an interaction involving a palpigrade in its natural habitat and the first record of *Metagonia* in Brazilian caves.

Little is known about the biology of species of *Metagonia* and of the spectrum of prey usually consumed by these spiders (Huber & Schüte 2009). A female of *M. osa* was observed feeding on an ant, and a male of the same species feeding on a cobweb spider (Theridiidae) (Huber & Schüte 2009). This study reports some new details about habitat, predation habits, one of the food items (Palpigradi) and some ethological information of *M. potiguar*. Furthermore, our study represents the documentation of a new cave-dwelling inhabitant of the genus, increasing the number of species of *Metagonia* associated with underground environments.

The order Palpigradi is one of the least known orders within Arachnida, and the large majority of publications associated with it focus on the taxonomy of the group. The small size of these arachnids hinders work on their biology and behavior, having been restricted so far to the work of Kováč et al. (2002), who was able to keep individuals of *E. spelaea* (Peyerimhoff 1902) over the course of four weeks in laboratory conditions. In spite of offering different types of prey to live specimens, Kováč et al. (2002) were unable to observe any individual capturing and feeding on them. According to Condé (1996), P. Weygoldt was able to observe laboratory-maintained palpigrades capturing small Collembola with the aid of their chelicerae. The interaction of these arachnids with other invertebrate species still remains unknown, and no ecological relationship in nature has been published.

Finally, this interaction is a clear indication that Palpigradi can be preyed upon by small spiders. The typical preference for interstitial habitats observed in many species of this group is maintained even in deep parts of caves. If this preference for such habitats were based only on the search for humid and shaded areas, one would not expect to find palpigrades sheltered under rocks in deep areas of caves, which are always aphotic and extremely humid. Therefore, the observed interaction raises the question whether the preference for interstitial microhabitats under rocks in caves may eventually be an answer to predation pressure.

ACKNOWLEDGMENTS

We would like to thank Paulo Rebelles Reis (EPAMIG-CTSM/EcoCentro Lavras) for use of the phase contrast microscope, Diego M. Bento for sending some specimens and CECAV/RN for logistic support during field work. The CNPq (National Counsel of Technological and Scientific Development from Brazil) provided some financial support for some of the collections (Process n. 477712/2006-1). This study was financially supported by grants from "Conselho Nacional de Desenvolvimento Científico e Tecnológico" (ADB, CNPq-Brazil # 300169/1996-5, and EOM, CNPq-Brazil # 141540/2007-9).

LITERATURE CITED

Barranco, P. & J.G. Mayoral. 2007. A new species of *Eukoenenia* (Palpigradi: Eukoeneniidae) from Morocco. Journal of Arachnology 35:318–324.

Barranco, P. & M.S. Harvey. 2008. The first indigenous palpigrade from Australia: a new species of *Eukoenenia* (Palpigradi: Eukoeneniidae). Invertebrate Systematics 22:227–233.

Christian, E. 2009. A new soil-dwelling palpigrade species from northern Italy (Palpigradi: Eukoeneniidae). Zootaxa 2136:59–68.

Condé, B. 1989. Palpigrades (Arachnida) endóges del'India et Sumatra. Revue Suisse de Zoologie 96:411–424.

Condé, B. 1993. Description du male de deux speces de Palpigrades. Revue Suisse de Zoologie 100:279–287.

Condé, B. 1996. Les Palpigrades, 1885–1995: acquisitions et lacunes. Revue Suisse de Zoologie, hors-série 1:87–106.

Condé, B. 1997. Description complémentaire du palpigrade brésilien *Eukoenenia janetscheki* Condé, 1993. Amazoniana 14:213–220.

Condé, B. 1998. Palpigradida. Pp. 913–920. *In* Encyclopaedia Biospeologica. Volume II. (C. Juberthie & V. Decu, eds.). Société Internationale de Biospeologie, Moulis (C.N.R.S.), France and Bucarest (Academie Rumanie), Romania.

Gertsch, W.J. 1986. The spider genus Metagonia (Araneae: Pholcidae) in North America, Central America, and the West Indies. Texas Memorial Museum, Speleological Monographs 1:39–62.

Harvey, M.S. 2003. Catalogue of the Smaller Arachnid Orders of the World: Amblypygi, Uropygi, Schizomida, Palpigradi, Ricinulei and Solifugae. CSIRO Publishing, Collingwood, Victoria, Australia.

Huber, B.A. 1997. On American *'Micromerys'* and *Metagonia* (Araneae, Pholcidae), with notes on natural history and genital mechanics. Zoologica Scripta 25:341–363.

Huber, B.A. 1998. Report of some pholcid spiders collected in Guatemala and Honduras (Araneae, Pholcidae). Revue Suisse de Zoologie 105:49–80.

Huber, B.A. 2000. New World pholcid spiders (Araneae: Pholcidae): a revision at generic level. Bulletin of the American Museum of Natural History 254:1–348.

Huber, B.A. 2004. Evidence for functional segregation in the directionally asymmetric male genitalia of the spider *Metagonia mariguitarensis* (Gonzalez-Sponga) (Pholcidae: Araneae). Journal of Zoology, London 262:317–326.

Huber, B.A., C.A. Rheims & A.D. Brescovit. 2005. Two new species of litter-dwelling *Metagonia* spiders (Araneae, Pholcidae) document both rapid and slow genital evolution. Acta Zoologica 86:33–40.

Huber, B.A. & A. Schütte. 2009. Preliminary notes on leaf-dwelling *Metagonia* spiders (Araneae: Pholcidae) in the Esquinas Rainforest near La Gamba, Costa Rica: leaf preference, mimesis, and web structure. Contributions to Natural History (Bern) 12:681–697.

Kováč, L., A. Mock, P. L'uptáčik & J.G. Palacios-Vargas. 2002. Distribution of *Eukoenenia spelea* (Peyerimhoff, 1902) (Arachnida, Palpigradida) in the Western Carpathians with remarks on its biology and behavior. Pp. 93–99. *In* Studies on Soil Fauna in Central Europe. (K. Tajovský, V. Balík & V. Pižl, eds.). Institute of Soil Biology, Academy of Science of the Czech Republic, České Budějovice, Czech Republic.

Král, J., L. Kováč, F. Št'áhlavský, L. Lonský & P. L'uptáčik. 2008. The first karyotype study in palpigrades, a primitive order of arachnids (Arachnida: Palpigradi). Genetica 134:79–87.

Krantz, G.W. & D.E. Walter. 2009. A Manual of Acarology. Third edition. Texas Tech University Press, Lubbock, Texas.

Mayoral, J.G. & P. Barranco. 2002. Palpígrados: Grandes desconocidos (Arachnida, Microthelyphonida). Revista Ibérica de Aracnologia 5:103–109.

Mello-Leitão, C. & R. Arlé. 1935. Considerações da ordem Palpigradi com a descrição de uma nova espécie. Anais da Academia Brasileira de Cie˙ncias 7:339–343.

Pepato, A.R., C.E.F. Rocha & J.A. Dunlop. 2010. Phylogenetic position of the acariform mites: sensitivity to homology assessment under total evidence. BMC Evolutionary Biology 10:1–23.

Pérez González, A. & B.A. Huber. 1999. *Metagonia debrasi* n. sp., the first species of the genus *Metagonia* Simon in Cuba (Pholcidae, Araneae). Revue Arachnologique 13:69–72.

Platnick, N.I. 2010. The World Spider Catalog, Version 10.5. American Museum of Natural History, New York. Online at http://research.amnh.org/entomology/spiders/catalog/index.html.

Souza, M.F.V.R. & R.L. Ferreira. 2010. *Eukoenenia* (Palpigradi: Eukoeneniidae) in Brazilian caves with the first troglobiotic palpigrade from South America. Journal of Arachnology 38: 415–424.

Souza, M.F.V.R. & R.L. Ferreira. 2011a. A new species of *Eukoenenia* (Palpigradi: Eukoeneniidae) from Brazilian iron caves. Zootaxa. 2886:31–38.

Souza, M.F.V.R. & R.L. Ferreira. 2011b. A new troglobitic *Eukoenenia* (Palpigradi: Eukoeneniidae) from Brazil. Journal of Arachnology 39:185–188.

Manuscript received 19 January 2011, revised 7 May 2011.

2011. The Journal of Arachnology 39:420–438

Morphological analysis of montane scorpions of the genus *Vaejovis* (Scorpiones: Vaejovidae) in Arizona with revised diagnoses and description of a new species

Garrett Brady Hughes[1]: Department of Life, Earth, and Environmental Sciences, West Texas A&M University, Canyon, Texas 79016, USA. E-mail: gbhughes@email.arizona.edu

Abstract. Several scorpions of the genus *Vaejovis* in Arizona are restricted in range to mountain-top forests. These scorpions, informally referred to as the "*vorhiesi* complex" are very similar morphologically, but their geographic distribution has attracted the attention of several researchers, resulting in the description of a few new species in recent years. However, these species were described from small sample sizes and were diagnosed with questionable characters that were not sufficiently analyzed. This study evaluates the morphology of scorpions of the "*vorhiesi* complex" from seven regions in Arizona to verify the validity of the species and their accompanying diagnoses. Morphological characters examined include morphometrics, hemispermatophores, size and shape of subaculear tubercles of the telson vesicle, pectinal tooth counts, pedipalp chela denticle counts, metasomal setal counts, development of metasomal carinae, and tarsal spinule counts. New diagnoses are given for previously described species (*V. vorhiesi* Stahnke 1940, *V. lapidicola* Stahnke 1940, *V. paysonensis* Soleglad 1973, *V. cashi* Graham 2007 and *V. deboerae* Ayrey 2009), which are considered valid, based on the morphological evidence gathered. A new species of *Vaejovis*, *V. electrum*, is described from the Pinaleño Mountains in Arizona.

Keywords: Morphometrics, discriminant function analysis, sky islands, *mexicanus* group

The family Vaejovidae is the most diverse and speciose group of scorpions in North America (Sissom 2000). Some species are known from as far north as southwestern Canada and as far south as Guatemala in Central America (Sissom & Francke 1981; Sissom 1989). Two qualities that contribute to this high diversity are the low dispersal capabilities and high substrate fidelity of vaejovids. There are, for example, vaejovid scorpions that specialize in rocky habitats and live in the cracks and crevices of rock faces (e.g., *Serradigitus* spp., *Vaejovis nitidulus* group) and others that are restricted to sandy habitats, including sand dunes (e.g., *Paruroctonus, Vejovoidus*) (Prendini 2001).

Within the family Vaejovidae, the genus *Vaejovis* is by far the largest, with 74 species, and is the third largest genus of scorpions in the world (see www.vaejovidae.com). Within the genus, there are five species groups: the *eusthenura* group, the *intrepidus* group, the *mexicanus* group, the *nitidulus* group, and the *punctipalpi* group. Several species are not placed in any of these groups. There is much doubt among current researchers that these groups, or the genus *Vaejovis* itself, represent monophyletic assemblages. Revisionary systematic work is being conducted to obtain a robust phylogeny of the family and a greater understanding of the relationships between species (www.vaejovidae.com).

Within the *mexicanus* group there is a collection of species informally referred to as the "*vorhiesi* complex" (although some exclude *V. vorhiesi* from the *mexicanus* group: Santibáñez-López & Francke 2010). The "*vorhiesi* complex" is a group of small (approximately 20–30 mm), brown, mottled scorpions that live in the mountains of the Madrean archipelago, a group of mountain "islands" found between the Sierra Madre Occidental range of northern Mexico and the Rocky Mountain range of the United States (Warshall 1994). These scorpions are generally found at elevations above 2100 m, where they dwell in the pine or oak litter of the mountain forests (Sissom 2000). The currently described species of the "*vorhiesi* complex" in Arizona include *V. vorhiesi* Stahnke 1940; *V. lapidicola* Stahnke 1940; *V. paysonensis* Soleglad 1973; *V. cashi* Graham 2007; and *V. deboerae* Ayrey 2009. Another species, *V. feti* Graham 2007, is known from the Black Range of New Mexico, but it may occur in Arizona as well because the Black Range is considered a part of the San Francisco Mountains, which extend into Arizona. Most recently, *V. montanus* was described from the Sierra Madre Occidental in Mexico (Graham 2010), but this description was published after completion of the current study so is not included in my analyses.

The fact that these scorpions are restricted to the mountain top forests has led to speculation that each isolated population is a distinct species (Graham 2007; Ayrey 2009). This hypothesis is derived from the understanding that isolated populations tend to diverge through time because of random genetic drift or selection for different traits. It is currently estimated that populations of the "*vorhiesi* complex" were isolated from one another around 10,000 years ago when forests covering most of Arizona retreated up the mountains coincident with the end of the most recent ice age (Anderson 1993; Maddison & McMahon 2000). Authors have described new species from these areas within the last few years based on dubious morphological differences (Graham 2007; Ayrey 2009). Almost all published species descriptions to date have been based on very low sample sizes: one male and one female specimen for *V. vorhiesi* (from different mountain ranges) (Stahnke 1940), two females for *V. lapidicola* (Stahnke 1940), seven females and four juveniles for *V. paysonensis* (Soleglad 1970), two females for *V. cashi* (Graham 2007), and a male and female for *V. feti* (although the author suggests that "many" were examined) (Graham 2007). Only the study by Ayrey (2009) utilized larger sample sizes, approximately 30 specimens including both males and females, for *V. deboerae*. Ayrey (2009) also listed 17 specimens of *V. vorhiesi* used in comparisons. Using robust

[1] Current Address: Department of Entomology, University of Arizona, 1140 E Campus Drive, Tucson, Arizona 85721, USA.

sample sizes is important in taxonomic work, especially when only considering morphological characters, because it reveals the extent of intraspecific variation. Without this knowledge, species may be described from characters that are not diagnostic of species-level differences. At the extreme, new species may even be described from variants of a previously described species. Furthermore, specimens should be from as many localities as possible because slight environmental differences could result in morphological differences.

The purpose of this study was to gather more complete data from a much larger sample of specimens and on a wider variety of morphological characters from seven geographically proximal groups of scorpions (mostly from mountain systems) in Arizona to assess the validity of previous species descriptions and discover non-overlapping, or at least minimally overlapping, characters that can distinguish populations or groups of populations.

Taxonomic History.—*Vaejovis vorhiesi* and *V. lapidicola* were first described by Stahnke (1940). *Vaejovis vorhiesi* was described from specimens collected in the Huachuca and Santa Catalina Mountains in southeastern Arizona. *Vaejovis lapidicola* was described from an area 1.6 km east of Flagstaff. Unfortunately, Stahnke's (1940) published descriptions were merely short paragraphs that provided few details of the species. One can discern differences between these two species from his published descriptions, but his unpublished dissertation (Stahnke 1939) clearly reveals the differences he considered most important in a dichotomous key. By examining the species descriptions one can find additional differences, such as differing numbers of pectinal lamellae with five to seven in *V. lapidicola* and six to eight in *V. vorhiesi*. Stahnke's (1939) dissertation yields two additional differences. The first difference is the relative length-to-width ratio of the fifth segment of the metasoma, with *V. lapidicola* having this segment more than twice as long as wide and *V. vorhiesi* with this segment equal to or less than twice as long as wide. Another distinction is that the intercarinal spaces of the ventral surface of the fifth metasomal segment differ in their granulation, with *V. lapidicola* having coarsely granular intercarinal spaces and *V. vorhiesi* having smooth to finely granular spaces (Stahnke 1939).

Soleglad (1973) created the *mexicanus* group of the genus *Vaejovis* and placed *V. lapidicola* and *V. vorhiesi* into this group. The *mexicanus* group was defined by the following characters: female genital operculum divided on posterior one-fifth; pedipalp chela fixed finger length equal to or longer than the pedipalp chela width; inner ventral carina of the palm of the chela "obsolete, suppressed, or well-developed"; trichobothria *ib* and *it* on the base of the finger and not on the palm; carapace indented on the anterior margin but not deeply bilobed; and ratio of total length to pectinal tooth count 1.91–2.95 for males and 1.87–3.50 for females. Soleglad (1973) described a new species, *V. paysonensis* from 40.23 km (25 mi) northeast of the city of Payson, Arizona. *Vaejovis paysonensis* was not compared to *V. lapidicola*, despite its closer proximity in both form and geography. However, Soleglad (1973) compared his new species to *V. vorhiesi*, distinguishing them by means of the following traits: seven inner accessory denticles on the pedipalp chela movable fingers in *V. paysonensis* and six in *V. vorhiesi*. There are 11–13 pectinal teeth for both males and females in *V. paysonensis* and 15 in males and 12–13 in females of *V. vorhiesi*. The ratio of chela palm width to chela length in *V. paysonensis* is 15/52 and in *V. vorhiesi* is 12/50. Finally, Soleglad (1973) reported lighter coloration in *V. paysonensis*.

Graham (2006) redescribed *V. lapidicola* from the two syntypes in poor condition and one other female. The major alteration made to the description is coloration, which may have changed in 48 years since the specimen was collected and preserved. In addition, he added measurement data that were lacking in the first published description, although Stahnke (1973) did include measurements in his unpublished dissertation. Graham (2006) identified *V. paysonensis* as the species most similar to *V. lapidicola* based on the possession of seven inner accessory denticles on the pedipalp chela movable finger. He distinguished *V. lapidicola* as having a more planate (flattened) carapace. Also, the ratios of carapace length over width, with width measured at the median eyes, are reported as 1.25 and 1.44 for *V. lapidicola* and *V. paysonensis*, respectively. There was no indication of whether these ratios are averages or from single specimens.

Graham (2007) described *V. cashi*, from the Chiricahua Mountains, and *V. feti*, from the Black Range in New Mexico, along with a redescription of *V. vorhiesi*. Graham (2007) distinguished *V. vorhiesi* from the other two species by its larger size, lighter pigment patterns, and the presence of 6–7 denticles on the third denticle row of the pedipalp chela movable finger instead of 8–9 as is found in *V. cashi* and *V. feti*. The latter two are diagnosed by coloration (*V. cashi* is red or mahogany and *V. feti* is brown) and by the presence (*V. cashi*) or absence (*V. feti*) of a subaculear tubercle of the telson.

The most recently described species of the "*vorhiesi* complex" in Arizona was *V. deboerae* (Ayrey 2009). *Vaejovis deboerae* is restricted to the Santa Catalina Mountains of Arizona. Ayrey (2009) presented a table comparing measurements and morphometric ratios using only type females of *V. vorhiesi*, *V. cashi*, and *V. feti*, and using the holotype of *V. deboerae* with two other specimens (a paratype male and female). However, the only measurements included from the two paratypes were total length and carapace length, and the only ratio used was metasomal length/carapace length. He used multiple specimens for pectinal tooth counts. Ayrey (2009) diagnosed *V. deboerae* from *V. vorhiesi*, *V. cashi*, and *V. feti* based on overall body size, apparently based on the measurements of only type specimens. He compared morphometric ratios of *V. deboerae* and *V. vorhiesi*, reporting differences in means of ratios, suggesting multiple specimens were measured, though no sample size was reported. *Vaejovis deboerae* was also indicated as being different from the others in having lighter legs and a darker body, heavier granulation, enlarged dorsolateral carinae of metasomal segment I, the presence of an enlarged spinoid denticle on the distal end of the dorsolateral carinae of metasomal segment IV, longer lateral inframedian carinae on metasomal segments II–III, and lateral inframedian carinae present on the distal 2/5 of metasomal segment IV. Ayrey (2009) compared pectinal tooth counts using the mean count of each population and performed student's *t*-tests pair-wise between *V. deboerae* and *V. vorhiesi, V. cashi, and V. feti*. All 3 tests were statistically significant, even though the means for *V. deboerae* and *V. vorhiesi* were 11.89 and 12.39, respectively, which, if rounded to the whole numbers that pectinal teeth are counted as, may both be considered 12 and therefore may not truly be diagnostic. Because only means are reported, no sense of the true overlap observed by Ayrey (2009) can be obtained.

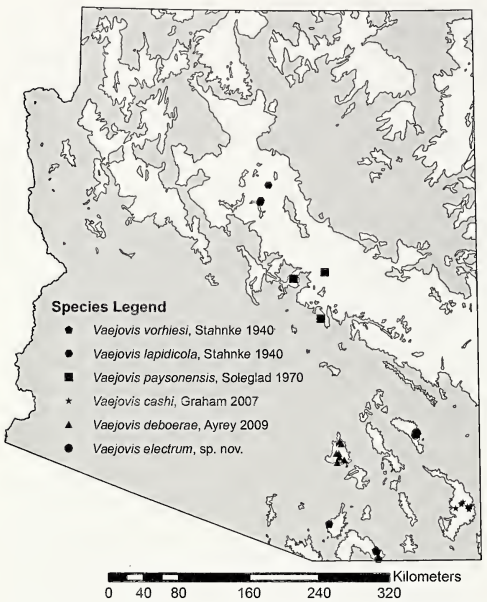


Figure 1.—Distribution map of montane scorpions of the genus *Vaejovis* found in Arizona. Each black shape represents a collecting locality. White areas represent forests in Arizona, usually above 1000 m. Species legend in lower left of map indicates which shapes represent localities for each of the six species.

METHODS

Specimens.—Specimens were borrowed from the American Museum of Natural History, New York (AMNH), the California Academy of Sciences, San Francisco (CAS), and W. David Sissom's personal collection (WDS). The specimens examined originated from six mountain ranges in Arizona: Chiricahua, Huachuca, Pinaleño, Santa Catalina, Santa Rita, and Sierra Ancha (Fig. 1). Specimens reported as being from "Payson, AZ" are grouped with the Sierra Ancha specimens because of their relatively close proximity to that range. I also examined specimens from the high elevation area around Flagstaff and Sedona (hereafter collectively referred to as "Sedona"). Each of these areas was used because each has a currently described species of the "*vorhiesi* complex" living there, except for the Pinaleño Mountains.

All data for the Huachuca and Santa Rita Mountains are reported separately to demonstrate the lack of diagnostic characters for those two groups and were also combined to aid in comparison of that species with other species. Combined data from the Huachuca and Santa Rita Mountains are denoted as Huachuca/Santa Rita in the tables.

Meristic Counts.—Pectinal tooth counts for males and females were collected from each population. I examined approximately 730 specimens for pectinal tooth data and recorded the number of times each count was present for each population.

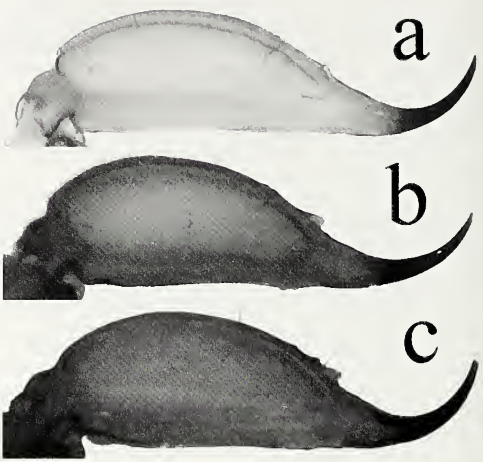


Figure 2.—Development of subaculear tubercles on the telson of *Vaejovis* scorpions. a. single poorly developed tubercle; b. single well-developed tubercle; c. multiple tubercles.

I counted the number of inner accessory denticles on the fixed and movable fingers of both pedipalp chelae for 20 specimens, 10 male and 10 female, from each population. In cases where 20 specimens were not available, as many as were available were counted. I also recorded the number of median denticles on each of the denticle subrows for 6–12 specimens from each of these populations, except Sedona.

Lateral inframedian carinae for metasomal segments II–IV were examined. All carinae began at the distal end of the segment but varied by how far they extended anteriorly. Each carina was categorized by the percentage of the segment it occupied.

Setal maps, containing information on the numbers and patterns of setae on the metasoma, are useful for distinguishing some closely related groups of scorpions (Yahia & Sissom 1996: see Discussion). I created metasomal setal maps for five specimens from each of the seven areas to see if consistent patterns were apparent between species or groups of species, with the intention of recording setal counts and drawing more setal maps if potentially distinguishing features were apparent. Numbers and positions of setae were so varied within species that no further counts were made because there was no prospect of finding distinguishing characters from the setal maps.

Tarsomere spinule counts were examined as described by McWest (2009).

Subaculear tubercles.—Subaculear tubercles were classified into three groups based on the number or development of the tubercle(s): "single poorly developed tubercle", "single well-developed tubercle", and "multiple tubercles" (Fig. 2). I classified individuals with a single bifurcate tubercle as having multiple tubercles. All telsons with multiple tubercles were grouped as "multiple tubercles". The remaining telsons with single tubercles were classified as being "well-developed" or "poorly developed" on the basis of the angle formed between

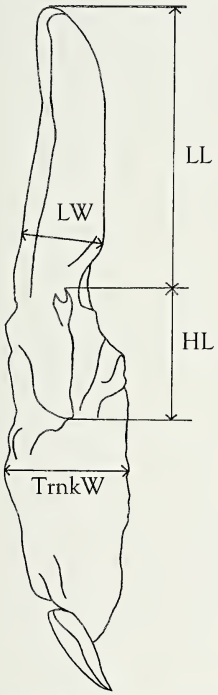


Figure 3.—Diagram of *Vaejovis* hemispermatophore showing measurements. Abbreviations: LL, lamina length; LW, lamina width; TrnkW, trunk width; HL, hook length.

the aculeus and the tip of the tubercle. I categorized tubercles with acute angles as "well-developed" and those with obtuse angles as "poorly developed".

Mensuration.—Right-side hemispermatophores were extracted and examined as described by Sissom et al. (1990: 458). Measurements of hemispermatophores were taken of the lamina length, lamina width, trunk width, and hook length for each of the hemispermatophores (Fig. 3). Lamina length was measured from the tip of the lamina to the top of the hooks. I measured lamina width as a line from the corner of the lamina perpendicular to the opposing lamina edge. Trunk width was measured across the widest part of the trunk with the lamina plane parallel with the plane of the microscope stage. In all measurements, the points were lined up in the same plane of focus to ensure accurate measurement of the distance between the points. Hook length was measured from the bottom of the trough to the top of the hooks. In cases where the hemispermatophore was damaged, I did not measure aspects that were likely to be affected by the damage. For example, the lamina length of laminas that were bent was not measured. Three ratios were constructed from these measurements: lamina length/lamina width, lamina length/hook length and trunk width/hook length.

I measured standard features of the scorpions as described by Sissom et al. (1990:452). It should be noted that the proper interpretation of this figure is that the measurement should be taken between the two points of the feature in contact with the parallel lines, not as a perpendicular measurement between the parallel lines.

A stage micrometer was used to calibrate the ocular scale in the microscope. All measurements were taken in millimeters. I took each measurement with the end points in the same plane of focus, which is necessary to take consistent measurements because the slightest degree of rotation can alter the apparent distance between the two points. Measurements were taken from 20 males and 20 females from each of the populations or as many as were available when there were less than 20. In total, 11 measurements were taken and eight ratios were calculated.

Statistics.—Percent overlap was calculated for each measurement and ratio in pair-wise fashion between each population. I calculated percent overlap by first taking the minimum and maximum values of a measurement or ratio from two different populations. Next, I took the difference between the larger of the two maximum values and the smaller of the two minimum values. This resulted in the overall range for that measurement or ratio. Then the larger of the minimum values was subtracted from the smaller of the maximum values. A positive value meant there was no overlap between the two populations. A negative value meant there was at least some degree of overlap between the two populations. If there was overlap, the difference between the larger minimum and smaller maximum was divided by the difference between the larger maximum and the smaller minimum (the total range) and multiplied by 100. Cases where the minimum and maximum of one population were between the minimum and maximum of the other population were considered as having 100% overlap.

Multiple pair-wise comparisons of data can inflate the type-I error rate. In other words, it makes it more likely to reject a true null hypothesis. Multivariate statistics prevent this phenomenon by considering all data simultaneously. I conducted canonical discriminant function analysis to see if there were differences between the measurements of the populations. The measurements used were carapace length, metasoma segment III length, metasoma segment III width, metasoma segment V length, metasoma segment V width, femur length, femur width, chela length, chela width, fixed finger length, and movable finger length. I conducted the analysis separately for females and males and used the base 10 logarithms of the measurements because the data were not normally distributed. My calculations were performed and figures and tables were created with SPSS 13.0 for Windows Student Version (Apache Software Foundation © 2000).

RESULTS

Meristic and qualitative characters.—Modal pectinal tooth counts were higher for males and females of the Huachuca and Santa Rita Mountains and lower for males and females of the Sierra Ancha Mountains (Table 1). Although pectinal tooth counts overlap greatly depending on whether a given count is expressed in a population, large sample sizes, such as those found in the Chiricahua Mountains, demonstrate that the mode is a useful character because there are typically far more

Table 1.—Distribution of pectinal tooth counts for montane *Vaejovis* scorpions sampled from seven areas in Arizona. The number of single pectines (a single specimen has two pectines) that display a given number of teeth in a geographic area can be found by locating the area on the left and reading across the table. Teeth from both pectines of a specimen were counted as independent pectines unless one was damaged or missing, in which case only teeth from the whole pectine were counted.

		Number of pectinal teeth per pectine									
	Group	9	10	11	12	13	14	15	16	Mean	Mode
Males	Huachuca						7	11	2	14.75	15
	Santa Rita					2	10	50	18	15.05	15
	Huachuca + Santa Rita					2	17	65	20	14.99	15
	Sedona			2	2	12	8			13.08	13
	Sierra Ancha				3	1				12.25	12
	Chiricahua			1	34	233	46	4	1	13.07	13
	Santa Catalina				1	11	6			13.28	13
	Pinaleño				2	28	6			13.11	13
Females	Huachuca			1	38	69				12.59	13
	Santa Rita			2	42	146	40	1		12.98	13
	Huachuca + Santa Rita			3	80	215	40	1		12.87	13
	Sedona	1	1	2	8	1				11.64	12
	Sierra Ancha		10	46	16					11.08	11
	Chiricahua		59	227	50	1				10.98	11
	Santa Catalina			16	44	7	2			11.93	12
	Pinaleño			29	62	5				11.75	12

specimens exhibiting the modal count than other counts, rather than the modal counts being represented by only a few more specimens compared to other counts.

For most groups, the number of specimens whose count of inner accessory denticles along both the movable and fixed pedipalp chela fingers differed from the mode is relatively few (Table 2). However, others have a greater a mount of variability. The Pinaleño and Santa Catalina specimens, for instance, have between 25% and 40% of their specimens differing from the modes. Aside from those two, the general trend observed is that the scorpions in the southeastern portion of Arizona have six and five inner accessory denticles for the pedipalp chela movable and fixed fingers, respectively, while the other scorpions have seven and six.

I found no distinguishing differences in the number of denticles within each median denticle subrow of the fixed and movable fingers of the pedipalp chelae because of the wide overlap between groups (Table 3).

Wide variability in lateral inframedian carinal development for metasomal segments II–IV rendered this character useless in distinguishing these groups from one another (Tables 4–6).

The Huachuca, Santa Rita, Sedona, and Sierra Ancha specimens had a majority of specimens with one poorly developed tubercle. The Pinaleño specimens mostly had

Table 2.—Distribution of inner accessory denticle counts on the pedipalp chela fingers for montane *Vaejovis* scorpions sampled from seven geographic areas in Arizona. The values in the middle of the table indicate the number chela fingers that display the given number of denticles (as labeled at the top of the column) found from a sample of individuals from a geographic area (as labeled at the left of the row). Mean and modal counts are presented on the right.

		# Inner accessory denticles						
Pedipalp chela finger	Group	4	5	6	7	8	Mode	Mean
Movable	Huachuca		5	35			6	5.9
	Santa Rita		6	34			6	5.9
	Huachuca + Santa Rita		11	69			6	5.9
	Sedona			4	35	1	7	6.9
	Sierra Ancha		2	1	37		7	6.9
	Chiricahua		3	37			6	5.9
	Santa Catalina		2	38			6	6
	Pinaleño	1		38			6	6
Fixed	Huachuca	1	39				5	5
	Santa Rita	1	39				5	5
	Huachuca + Santa Rita	2	78				5	5
	Sedona			40			6	6
	Sierra Ancha		2	38			6	6
	Chiricahua	2	38				5	5
	Santa Catalina		11	29			6	5.7
	Pinaleño		24	16			5	5.4

Table 3.—Ranges in the number of denticles found on each subrow of the median denticles row on the pedipalp chela fingers of montane *Vaejovis* scorpions from six geographic areas in Arizona. Each column of numbers represents a different subrow of median denticles and columns are listed left to right from most distal to most proximal. Note the variation and overlap between populations.

Group	Movable finger						Fixed finger						Sample size
	Distal end			Proximal end			Distal end			Proximal end			
Huachuca	0–2	5–8	7–10	8–10	7–10	16–25	4–6	6–9	7–9	6–9	7–10	14–24	11
Santa Rita	1–2	5–7	6–10	7–10	7–10	16–27	3–7	5–8	6–10	6–9	7–9	13–27	10
Sierra Ancha	1–2	6–8	8–10	8–11	8–10	19–25	5–8	7–9	7–10	6–9	7–9	15–22	6
Chiricahua	0–2	4–7	6–9	7–9	7–9	18–24	4–6	5–7	6–8	6–8	6–9	12–18	12
Santa Catalina	0–2	6–8	7–9	7–9	8–0	19–28	4–7	6–9	7–9	5–9	6–10	14–26	10
Piñaleno	0–2	4–7	7–9	6–9	6–11	17–27	2–6	6–7	6–9	6–8	7–10	1–29	10

multiple tubercles. The Chiricahuas had about half with multiple tubercles and half with well-developed tubercles, but none with poorly developed tubercles. The Santa Catalina specimens mostly had a single well-developed tubercle (Table 7).

The setal positioning as determined from the setal maps varied widely, and no distinguishing differences were found from it (Fig. 6). Tarsomere II spinule counts also appeared inconsistent and counts overlapped greatly between populations.

Morphometric characters.—Gross morphology of hemispermatophores appeared quite variable. I found many potential characters to be absent from specimens within a population but present in specimens from other populations. However, ratios of measurements from the hemispermatophores did reveal some differences. In particular, the Chiricahua specimens had much shorter laminas relative to the hook length. This ratio was consistently smaller and non-overlapping with any other group (Table 8).

Female measurements and ratios seemed less able to distinguish species than male measurements and ratios (Tables 9, 10). Perhaps the most frequent distinguishing difference between two species is the metasomal segment III length-over-width ratio. Chela length-over-width ratios were also informative.

Discriminant function analysis.—The discriminant function analyses created six functions because there were seven populations. Of these, the first two are responsible for most of the differences between groups (Figs. 4, 5). For the females, function 1 was most highly correlated with metasoma segment III width, but none of the correlations between function 1 and the measured features were very high. Function 2, however, was very highly correlated with all the measured features. For the males, function 1 was most highly correlated with chela width. Function 2 was highly correlated with all the remaining measured features, but of those the two metasomal length measurements contributed the most. The male groups were separated with little overlap when plotted. The groups with the most overlap were Santa Rita, Santa Catalina, and Huachuca, which is interesting because these mountain ranges are fairly close to one another. The plot of female specimens had a lot more overlap. The Santa Catalina group was the only one that did not overlap with any other group. SPSS also reclassified all specimens using the discriminant functions it created (Tables 11, 12). The male reclassification had a higher percent of correct reclassification (95.7%) than the female reclassification (86.8%). This was likely an effect of the difference in-group overlap mentioned above.

DIAGNOSIS

The following diagnoses refer to the currently described *mexicanus* group scorpions from Arizona and use the scientific names. For these diagnoses, my study locations refer to the following species: Huachuca = *V. vorhiesi* in part; Santa Rita = *V. vorhiesi* in part; Huachuca/Santa Rita = *V. vorhiesi* using combined data from the Huachucas and Santa Ritas; Sedona = *V. lapidicola*; Sierra Ancha = *V. paysonensis*; Chiricahua = *V.*

Table 4.—Distribution of development of lateral inframedian carina of metasomal segment II on montane *Vaejovis* scorpions sampled from seven geographic areas in Arizona. Carinal development is expressed as percent of sample size exhibiting a given amount of carinal development. Development of the lateral inframedian carina of metasomal segment II is expressed as proportion of the segment that has the carina present. All lateral inframedian carinae begin at the posterior end and extend anteriorly. For example, 14.3% of the 21 Santa Rita specimens had carinae that extended half way along the length of the segment from the posterior end.

Group	% Specimens with inframedian carina II extending anteriorly												Sample size
	0	1/5	1/4	1/3	2/5	1/2	3/5	2/3	3/4	4/5	5/6	1/1	
Huachuca							27.7		4.5	59.1	4.5	9.1	22
Santa Rita						14.3	9.5			47.6	23.8	4.8	21
Huachuca + Santa Rita						7.0	16.3		2.3	53.5	14.0	7.0	43
Sedona			11.1	11.1	22.2	22.2	11.1		11.1	11.1			9
Sierra Ancha				4.5	13.6	31.8	13.6			27.3	4.5	4.5	22
Chiricahua			4.5			3.2	4.5	13.6	13.6	22.7	9.1		22
Santa Catalina					4.2	4.2	8.3			50.0	4.2	29.2	24
Pinaleño					4.3			8.7	4.3	47.8	26.1	8.7	23

Table 5.—Distribution of development of lateral inframedian carina of metasomal segment III on montane *Vaejovis* scorpions sampled from seven geographic areas in Arizona. Carinal development is expressed as percent of sample size exhibiting a given amount of carinal development. Development of the lateral inframedian carina of metasomal segment III is expressed as proportion of the segment that has the carina present. All lateral inframedian carinae begin at the posterior end and extend anteriorly.

Group	% Specimens with inframedian carina IV extending anteriorly												Sample size
	0	1/5	1/4	1/3	2/5	1/2	3/5	2/3	3/4	4/5	5/6	1/1	
Huachuca	50.0	13.6			22.7	9.1				4.5			22
Santa Rita	28.6	4.8	4.8		28.6	9.5	9.5			14.3			21
Huachuca + Santa Rita	39.5	9.3	2.3		25.6	9.3	4.7			9.3			43
Sedona	88.9	11.1											9
Sierra Ancha	50.0		13.6	9.1	13.6	9.1				4.5			22
Chiricahua	7.7		1.5	23.1	15.4	15.4			15.4		7.7		22
Santa Catalina	29.2	4.2			33.3	4.2				25.0			24
Pinaleño	26.1	4.3	8.7		8.7	27.1			8.7	21.7			23

cashi; Santa Catalina = *V. deboerae*. A new species from the Pinaleño Mountains is described following the other diagnoses.

Vaejovis vorhiesi Stahnke 1940

Vejovis vorhiesi Stahnke 1940:102 (original description); Soleglad 1973:359, 361, 363, 364; Stahnke 1974:135.

Vaejovis vorhiesi: Sissom 1991:221–222; Sissom 1997:13; Kovarík 1998:148; Graham 2006:3, 6; Graham 2007:1–6, 9, 10, 13; Ayrey 2009:1, 3, 5–9, figs. 7, 9, 12, 13.

Type material.—Lectotype: adult female, Miller Canyon (31°24′N, 110°17′W), Huachuca Mountains, Cochise County, Arizona, USA (CAS Type No. 15172); not examined. A second specimen (a paralectotype), a male from the Santa Catalina Mountains, is referable to *V. deboerae* Ayrey 2009.

Material examined.—USA: *Arizona*: Cochise County, Huachuca Mountains: Ramsey Canyon, 31°26′N, 110°18′W, 10–15 July 1941, A.B. Klots, 1 male (AMNH); Montezuma Pass, 31°21′N, 110°17′W, 1829 m, 4 June 1952, M. Cazier, W. Gertsch & R. Schrammel, 1 female (AMNH); Sierra Vista, 31°32′N, 110°16′W, 2134 m, under rocks, 17 July 1971, G. Bawden, 3 females (AMNH); Carr Canyon, 31°26′N, 110°17′W, 3 June 1952, M. Cazier, W. Gertsch & R. Schrammel, 2 males, 19 females, 1 juvenile (AMNH); Carr Canyon Rd., 1.8 km NNE Carr Peak, 31°25′N, 110°17′W, 2195 m, 19 June 1976, 2 females (AMNH); Carr Canyon, 31°26′N, 110°17′W, 2289 m, 31 July 1949, W.J. & J.W. Gertsch, 3 males, 13 females (AMNH); Upper Carr Canyon, 31°25′N, 110°18′W, 22 July 1955, W.J. Gertsch, 3 males, 7 females (AMNH); Lower Carr Canyon, 31°26′N, 110°17′W, 21 July 1955, W.J. Gertsch, 1 female (AMNH); Carr Canyon, in pines, 31°25′N, 110°17′W, 9 May 1961, W.J. Gertsch, 1 male (AMNH); 1.6 km W of Montezuma Pass, 31°21′N, 110°17′W, 6 September 1950, 2 females (AMNH); Coronado National Forest, Carr Canyon, Carr Canyon Road, rocky road cut slope, 31°26.069′N, 110°16.909′W, 1972 m, 21 June 2006, W. Savary, R. Mercurio, 2 males (AMNH/AMNH-ARA 00002511); Coronado National Forest, Carr Canyon, Carr Canyon Road, rocky road cut slope, 31°25.909′N, 110°17.053′W, 2112 m, 21 June 2006, W. Savary, R. Mercurio, 2 males, 1 female (AMNH/AMNH-ARA 00002516); Coronado National Forest, Carr Canyon, Carr Canyon Road, rocky road cut slope, 21 June 2006, W. Savary, R. Mercurio: 31°25.946′N, 110°17.052′W, 2061 m, 2 females (AMNH-ARA 00002512) & 31°25.812′N, 110°17.208′W, 2188 m, 3 males, 5 females, 2 subadult males, 1 juvenile (AMNH/AMNH-ARA 00002508)(AMNH). Santa Cruz Co., Santa Rita Mountains: Box Canyon, 31°47′N, 110°46′W, 29 August 1952, B. Malkin, 1 female (AMNH); Madera Canyon, 31°42N, 110°52′W, 7 June 1952, M. Cazier, W. Gertsch, R. Schrammel, 3 males, 41 females, 1 juvenile (AMNH) & 31 July 1952, Nutting, Warner, 1 female (AMNH) & O. Bryant, 1 female, 1 juvenile (AMNH); along trail to Mt. Wrightson, 31°42N, 110°52′W, 21 September 1970, R.C.A. Rice, 23 males, 20 females, 7 juveniles

Table 6.—Distribution of development of lateral inframedian carina of metasomal segment IV on montane *Vaejovis* scorpions sampled from seven geographic areas in Arizona. Carinal development is expressed as percent of sample size exhibiting a given amount of carinal development. Development of the lateral inframedian carina of metasomal segment IV is expressed as proportion of the segment that has the carina present. All lateral inframedian carinae begin at the posterior end and extend anteriorly.

Group	% Specimens with inframedian carina III extending anteriorly												Sample size
	0	1/5	1/4	1/3	2/5	1/2	3/5	2/3	3/4	4/5	5/6	1/1	
Huachuca						9.1	22.7			59.1	4.5	4.5	22
Santa Rita						9.5	9.5		9.5	52.4	14.3	4.8	21
Huachuca + Santa Rita						9.3	16.3		4.7	55.8	9.3	4.7	43
Sedona			33.3	33.3		33.3							9
Sierra Ancha			13.6	4.5	40.9	13.6	9.1			13.6	4.5		22
Chiricahua		4.5	4.5	18.2		27.3		4.5	13.6	18.2	9.1		22
Santa Catalina					8.0	12.0	8.0			52.0	8.0	12.0	24
Pinaleño			4.3		13.0	4.3	8.7	4.3	17.4	26.1	17.4	4.3	23

Table 7.—Development of subaculear tubercles in montane *Vaejovis* sampled from seven geographic areas in Arizona expressed as percentage of specimens examined from each area that displayed a given condition of subaculear tubercle. Sample sizes of specimens examined from each area are given on the right.

	% Sample whose telson exhibits each state of subaculear development			
Group	Multiple tubercles	1 Well-developed	1 Poorly developed	Sample size
Huachuca	0	0	100	85
Santa Rita	1	0	99	102
Huachuca + Santa Rita	1	0	99	187
Sedona	3	7	90	30
Sierra Ancha	20	8	72	36
Chiricahua	50	50	0	107
Santa Catalina	22	65	13	43
Pinaleño	77	20	3	61

(AMNH) & 22 August 1966, S.C. Williams, 3 males (CAS); Big Rock Camp, 31°42N, 110°52′W, 10 September 1941, W. Ivie, 1 female (AMNH); Roundup Camp, 31°42′N, 110°52′W, 11 September 1941, W. Ivie, 2 females, 12 juveniles (AMNH) & 23 March 1960, W.J Gertsch, W. Ivie & R. Schrammel, 12 females (AMNH) & 27 July 1949, W.J. & J.W. Gertsch, 2 males, 7 females (AMNH) & 27 July 1949, W.J. & J.W. Gertsch, 5 males, 15 females (AMNH) & 15 August 1955, W.J. Gertsch, 1 male, 1 female (AMNH) & 13 September 1963, W.J. Gertsch, 1 male, 3 females (AMNH) & 19 July 1962, W.J. Gertsch, 1 male, 3 females (AMNH) & 19 July 1949, W.J. Gertsch, 1 male, 3 females (AMNH); Madera Canyon, 31°42N, 110°52′W, 29 March 2008, B. Anderson & D. Crump, 31°42.875′N, 110°52.6625′W, 1 subadult female, 1 female (AMNH/AMNH LP 8336); above Mt. Wrightson Trailhead Parking, 31°42′N, 110°52′W, 25 July 2008, H.M. Burrell & K.J. McWest, 31°42.72666′N110°52.43832′W, 2 females (AMNH/AMNH LP 8960). Pima County, Santa: Cave Creek Canyon into Florida Canyon, trail at end of Gardner Canyon Road, 20 July 2008, K. Ksepka & M. Rubio, 1 female, (AMNH/AMNH LP 8931).

Diagnosis.—Specimens from the Huachuca Mountains and the Santa Rita Mountains can be considered as a single species, because there are no characters that distinguish one from the other. This species is identified as *V. vorhiesi* because the lectotype of the species selected by Graham (2007) was taken from the Huachuca Mountains. It can be distinguished from the other scorpions in this group by having higher pectinal tooth counts with male mode 15, range 13–16 and female mode 13, range 11–15.

Vaejovis vorhiesi can be distinguished from *V. lapidicola* and *V. paysonensis* by having fewer inner accessory denticles on the pedipalp chela fingers with 5 on fixed finger (6 in *V. lapidicola* and *V. paysonensis*) and 6 on movable finger (7 in *V. lapidicola* and *V. paysonensis*). *Vaejovis vorhiesi* can be further distinguished from *V. lapidicola* by the following features (*V. lapidicola* features follow in parentheses): stouter metasoma segment III, with length/width ratio ranging from 2.40–3.19

Table 8.—Hemispermatophore ratios that overlap by 10% or less between two groups of montane *Vaejovis* scorpions grouped by seven geographic areas in Arizona. Actual percent overlap is listed in the column on the right.

Male hemispermatophore ratios with 10% overlap or less			
Group 1	Group 2	Measurement or ratio	% Overlap
Huachuca	Sierra Ancha	Lamina L/Lamina W	0
Huachuca	Sierra Ancha	Lamina L/Hook L	0
Huachuca	Sierra Ancha	Trunk W/Hook L	2.93
Huachuca	Chiricahua	Lamina L/Hook L	0
Santa Rita	Sedona	Lamina L/Lamina W	0
Santa Rita	Sierra Ancha	Lamina L/Hook L	0
Santa Rita	Sierra Ancha	Trunk W/Hook L	2.21
Santa Rita	Chiricahua	Lamina L/Lamina W	0
Santa Rita	Chiricahua	Lamina L/Hook L	0
Huachuca/Santa Rita	Sierra Ancha	Lamina L/Lamina W	0
Huachuca/Santa Rita	Chiricahua	Lamina L/Hook L	0
Sedona	Sierra Ancha	Trunk W/Hook L	0
Sedona	Chiricahua	Lamina L/Hook L	0
Sedona	Chiricahua	Trunk W/Hook L	0
Sierra Ancha	Chiricahua	Lamina L/Hook L	0
Sierra Ancha	Santa Catalina	Lamina L/Hook L	2.71
Chiricahua	Santa Catalina	Lamina L/Hook L	0
Pinaleño	Santa Rita	Lamina L/Hook L	0
Pinaleño	Sedona	Trunk W/Hook L	0
Pinaleño	Chiricahua	Lamina L/Hook L	0

Table 9.—Female measurements and ratios that overlap by 10% or less between two groups of montane *Vaejovis* scorpions grouped by seven geographic areas in Arizona. Actual percent overlap is listed in the column on the right.

Female measurements/ratios with 10% overlap or less			
Group 1	Group 2	Measurement or ratio	% Overlap
Huachuca	Sedona	III L/III W	6.35
Huachuca	Sierra Ancha	III W	7.88
Huachuca	Sierra Ancha	ChL/ChW	1.34
Huachuca	Sierra Ancha	FFL/ChL	0
Huachuca	Chiricahua	FFL/CaL	9.14
Huachuca	Chiricahua	FFL/ChL	6.2
Huachuca	Santa Catalina	CaL	0
Huachuca	Santa Catalina	III L	9.73
Huachuca	Santa Catalina	ChL	4.61
Huachuca	Santa Catalina	ChW	0
Huachuca	Santa Catalina	FFL	6.12
Santa Rita	Sedona	III L/III W	0
Santa Rita	Sierra Ancha	ChL/ChW	1.5
Santa Rita	Sierra Ancha	MFL/ChW	0
Santa Rita	Sierra Ancha	FFL/ChL	7.4
Santa Rita	Chiricahua	FFL/CaL	5.96
Santa Rita	Santa Catalina	CaL	0
Santa Rita	Santa Catalina	V L	8.69
Santa Rita	Santa Catalina	ChL	4.65
Santa Rita	Santa Catalina	ChW	0
Santa Rita	Santa Catalina	FFL	9.76
Huachuca/Santa Rita	Sedona	III L/III W	6.06
Huachuca/Santa Rita	Sierra Ancha	ChL/ChW	1.34
Huachuca/Santa Rita	Sierra Ancha	FFL/ChL	7.4
Huachuca/Santa Rita	Chiricahua	FFL/CaL	7.99
Huachuca/Santa Rita	Santa Catalina	CaL	0
Huachuca/Santa Rita	Santa Catalina	ChL	4.61
Huachuca/Santa Rita	Santa Catalina	ChW	7.17
Huachuca/Santa Rita	Santa Catalina	FFL	9.44
Sedona	Sierra Ancha	III L/III W	4.03
Sierra Ancha	Santa Catalina	CaL	0
Sierra Ancha	Santa Catalina	III L	0
Sierra Ancha	Santa Catalina	III W	0
Sierra Ancha	Santa Catalina	V W	0.22
Sierra Ancha	Santa Catalina	ChL	8.43
Sierra Ancha	Santa Catalina	FFL	0.19
Sierra Ancha	Santa Catalina	MFL	8.19
Chiricahua	Sedona	III L	3.15
Chiricahua	Sedona	FemL	7.46
Chiricahua	Sedona	ChL	5.05
Chiricahua	Sedona	FFL	7.59
Chiricahua	Sedona	FFL/CaL	0
Chiricahua	Sedona	III L/III W	0
Chiricahua	Santa Catalina	CaL	0
Chiricahua	Santa Catalina	III L	0
Chiricahua	Santa Catalina	III W	3.68
Chiricahua	Santa Catalina	V L	0
Chiricahua	Santa Catalina	V W	0
Chiricahua	Santa Catalina	FemL	4.14
Chiricahua	Santa Catalina	FemW	6.96
Chiricahua	Santa Catalina	ChL	0
Chiricahua	Santa Catalina	ChW	0
Chiricahua	Santa Catalina	FFL	0
Chiricahua	Santa Catalina	MFL	0.39
Pinaleño	Sedona	III L/III W	0
Pinaleño	Chiricahua	V W	7.59
Pinaleño	Santa Catalina	CaL	8.56
Pinaleño	Santa Catalina	V L	5.13
Pinaleño	Santa Catalina	ChL	4.74
Pinaleño	Santa Catalina	ChW	9.63

(3.15–3.78) in females and 0.95–1.2 (1.20–1.37) in males; more slender pedipalps in males, with chela length/width ratio 4.34–5.54 (3.78–4.25); smaller size of males in the following measurements: carapace length 2.40–3.19 (3.15–3.78), metasoma III length 1.35–1.86 (1.80–2.28), femur length 2.05–2.75 (2.80–3.43), chela length 3.35–4.54 (4.94–6.16), chela width 0.71–0.97 (1.23–1.16), fixed finger length 1.63–2.3 (2.42–3.19), movable finger length 2.05–2.92 (3.01–3.85). *Vaejovis vorhiesi* can be further distinguished from *V. paysonensis* by the following characters (*V. paysonensis* characters follow in parentheses): chela more slender with chela length/width 4.24–4.95 (3.70–4.25) in females and 4.34–5.54, (3.68–3.91) in males; hemispermatophore lamina more slender with lamina length/width ratio 4.25–4.63 (3.50–4.25); male chela palm narrower with chela width 0.71–0.97 (1.13–1.13).

Vaejovis vorhiesi can be distinguished from *V. cashi* by the following characters (*V. cashi* characters follow in parentheses): subaculear tubercle present only as a low mound (well-developed and/or multiple tubercles present); larger size in all male measurement lengths except carapace length, larger hemispermatophore lamina length/hook length ratio 2.35–3.09 (1.93–2.00).

Vaejovis vorhiesi can be distinguished from *V. deboerae* by the following characters (*V. deboerae* characters follow in parentheses): modal count of chela fixed finger inner accessory denticles 5 (6); subaculear tubercles present only as a low mound (present 14% of the time as low mound, more often well-developed or present as multiple tubercles); carapace length shorter with 3.10–3.80 (4.00–5.24) in females and 2.40–3.19 (3.10–3.66) in males; chelae smaller with length 4.65–5.44 (5.28–8.13) in females and width 0.99–1.23 (1.26–1.90) in females, 0.71–0.97 (0.96–1.23) in males.

Distribution.—*Vaejovis vorhiesi* is known from the Huachua and Santa Rita Mountains, Cochise County and Santa Cruz County, in southeastern Arizona, USA.

Vaejovis lapidicola Stahnke 1940

Vejovis lapidicola Stahnke 1940:102 (original description); Stahnke 1974:135.

Vaejovis lapidicola: Kovarik 1998:147; Graham 2006:1–6, figs. 1–12; Graham 2007:1, 3, 13.

Type material.—Syntypes: 3 females (CAS, Type No. 15171, HLS no. 74.0, HLS no. 71.1), 1 male (CAS, Type No. 10170), 1.6 km E of Flagstaff, Coconino County, Arizona, USA.

Material examined.—USA: *Arizona*: Coconino County: Flagstaff, 35°12′N, 111°38′W, 4 June 1949, A.R. Phillips, 2 females (AMNH) & 2164 m, MNA, July 1947, J. Ferriss, 1 male (AMNH) & 17 June 1943, 1 female (AMNH); ca. 24 km N Sedona on US 89A, 35°02′N, 111°44′W, 19 August 2009, T. Anton, Casper & W.D. Sissom, 3 males, 1 female (AMNH);

Table 10.—Male measurements and ratios that overlap by 10% or less between two groups of montane *Vaejovis* scorpions grouped by seven geographic areas in Arizona. Actual percent overlap is listed in the column on the right.

Male measurements/ratios with 10% overlap or less			
Group 1	Group 2	Measurement or ratio	% Overlap
Huachuca	Sedona	CaL	2.88
Huachuca	Sedona	III L	7.44
Huachuca	Sedona	FemL	0
Huachuca	Sedona	ChL	0
Huachuca	Sedona	ChW	0
Huachuca	Sedona	FFL	0
Huachuca	Sedona	MFL	0
Huachuca	Sedona	ChL/ChW	0
Huachuca	Sedona	MFL/ChW	4.94
Huachuca	Sierra Ancha	ChW	0
Huachuca	Sierra Ancha	ChL/ChW	0
Huachuca	Sierra Ancha	MFL/ChW	0
Huachuca	Sierra Ancha	CaL/V L	0
Huachuca	Chiricahua	CaL	7.04
Huachuca	Chiricahua	III L	0
Huachuca	Chiricahua	V L	0
Huachuca	Chiricahua	V W	8.15
Huachuca	Chiricahua	FemL	0
Huachuca	Chiricahua	FemW	4.89
Huachuca	Chiricahua	ChL	3.32
Huachuca	Chiricahua	FFL	4.78
Huachuca	Chiricahua	MFL	0.29
Huachuca	Santa Catalina	CaL	7.37
Huachuca	Santa Catalina	ChW	1.75
Huachuca	Santa Catalina	ChL/ChW	4.11
Santa Rita	Sedona	CaL	0
Santa Rita	Sedona	III L	0
Santa Rita	Sedona	V L	0
Santa Rita	Sedona	V W	6.6
Santa Rita	Sedona	FemL	0
Santa Rita	Sedona	FemW	0
Santa Rita	Sedona	ChL	0
Santa Rita	Sedona	ChW	0
Santa Rita	Sedona	FFL	0
Santa Rita	Sedona	MFL	0
Santa Rita	Sedona	ChL/ChW	0
Santa Rita	Sedona	MFL/ChW	0
Santa Rita	Sedona	FFL/CaL	0
Santa Rita	Sedona	III L/III W	0
Santa Rita	Sierra Ancha	ChL	0
Santa Rita	Sierra Ancha	ChW	0
Santa Rita	Sierra Ancha	ChL/ChW	0
Santa Rita	Sierra Ancha	MFL/ChW	0
Santa Rita	Sierra Ancha	V L/V W	4.51
Santa Rita	Sierra Ancha	CaL/V L	0
Santa Rita	Chiricahua	III L	7.24
Santa Rita	Chiricahua	V L	8.54
Santa Rita	Chiricahua	FemL	4.99
Santa Rita	Chiricahua	FFL	4.26
Santa Rita	Chiricahua	MFL	7.77
Santa Rita	Chiricahua	V L/V W	8.66
Santa Rita	Chiricahua	CaL/V L	7.13
Santa Rita	Santa Catalina	CaL	0
Santa Rita	Santa Catalina	III L	0
Santa Rita	Santa Catalina	III W	0
Santa Rita	Santa Catalina	V L	0
Santa Rita	Santa Catalina	V W	0

Table 10.—Continued.

Male measurements/ratios with 10% overlap or less			
Group 1	Group 2	Measurement or ratio	% Overlap
Santa Rita	Santa Catalina	FemL	9.89
Santa Rita	Santa Catalina	FemW	0
Santa Rita	Santa Catalina	ChL	0
Santa Rita	Santa Catalina	ChW	0
Santa Rita	Santa Catalina	FFL	1.06
Huachuca/Santa Rita	Sedona	CaL	2.72
Huachuca/Santa Rita	Sedona	III L	6.76
Huachuca/Santa Rita	Sedona	FemL	0
Huachuca/Santa Rita	Sedona	ChL	0
Huachuca/Santa Rita	Sedona	ChW	0
Huachuca/Santa Rita	Sedona	FFL	0
Huachuca/Santa Rita	Sedona	MFL	0
Huachuca/Santa Rita	Sedona	ChL/ChW	0
Huachuca/Santa Rita	Sedona	MFL/ChW	4.7
Huachuca/Santa Rita	Sierra Ancha	ChW	0
Huachuca/Santa Rita	Sierra Ancha	ChL/ChW	0
Huachuca/Santa Rita	Sierra Ancha	MFL/ChW	0
Huachuca/Santa Rita	Sierra Ancha	CaL/V L	0
Huachuca/Santa Rita	Chiricahua	III L	6.12
Huachuca/Santa Rita	Chiricahua	V L	6.67
Huachuca/Santa Rita	Chiricahua	FemL	4.97
Huachuca/Santa Rita	Chiricahua	ChL	7.89
Huachuca/Santa Rita	Chiricahua	FFL	4.78
Huachuca/Santa Rita	Chiricahua	MFL	7.77
Huachuca/Santa Rita	Santa Catalina	CaL	6.92
Huachuca/Santa Rita	Santa Catalina	ChW	1.75
Sedona	Sierra Ancha	CaL	0
Sedona	Sierra Ancha	III L	0
Sedona	Sierra Ancha	V L	0
Sedona	Sierra Ancha	V W	3.25
Sedona	Sierra Ancha	FemL	0
Sedona	Sierra Ancha	FemW	0
Sedona	Sierra Ancha	ChL	0
Sedona	Sierra Ancha	ChW	0
Sedona	Sierra Ancha	FFL	0
Sedona	Sierra Ancha	MFL	0
Sedona	Sierra Ancha	FFL/CaL	5.03
Sedona	Sierra Ancha	III L/III W	0
Sedona	Sierra Ancha	CaL/V L	0
Sedona	Chiricahua	CaL	0
Sedona	Chiricahua	III L	0
Sedona	Chiricahua	III W	0
Sedona	Chiricahua	V L	0
Sedona	Chiricahua	VW	0
Sedona	Chiricahua	FemL	0
Sedona	Chiricahua	FemW	0
Sedona	Chiricahua	ChL	0
Sedona	Chiricahua	ChW	0
Sedona	Chiricahua	FFL	0
Sedona	Chiricahua	MFL	0
Sedona	Chiricahua	FFL/CaL	0
Sedona	Chiricahua	III L/III W	0
Sedona	Santa Catalina	ChW	0.54
Sierra Ancha	Chiricahua	CaL	0
Sierra Ancha	Chiricahua	III L	0
Sierra Ancha	Chiricahua	III W	0
Sierra Ancha	Chiricahua	V L	0
Sierra Ancha	Chiricahua	V W	0
Sierra Ancha	Chiricahua	FemL	0
Sierra Ancha	Chiricahua	FemW	0

Table 10.—Continued.

Male measurements/ratios with 10% overlap or less			
Group 1	Group 2	Measurement or ratio	% Overlap
Sierra Ancha	Chiricahua	ChL	0
Sierra Ancha	Chiricahua	ChW	0
Sierra Ancha	Chiricahua	FFL	0
Sierra Ancha	Chiricahua	MFL	0
Sierra Ancha	Chiricahua	ChL/ChW	0
Sierra Ancha	Chiricahua	FFL/CaL	0
Sierra Ancha	Santa Catalina	CaL	0
Sierra Ancha	Santa Catalina	III L	0
Sierra Ancha	Santa Catalina	III W	0
Sierra Ancha	Santa Catalina	V L	0
Sierra Ancha	Santa Catalina	V W	0
Sierra Ancha	Santa Catalina	FemL	0
Sierra Ancha	Santa Catalina	FemW	0.38
Sierra Ancha	Santa Catalina	ChL/ChW	0
Sierra Ancha	Santa Catalina	MFL/ChW	0
Santa Catalina	Chiricahua	CaL	0
Santa Catalina	Chiricahua	III L	0
Santa Catalina	Chiricahua	III W	0
Santa Catalina	Chiricahua	V L	0
Santa Catalina	Chiricahua	V W	0
Santa Catalina	Chiricahua	FemL	0
Santa Catalina	Chiricahua	FemW	0
Santa Catalina	Chiricahua	ChL	0
Santa Catalina	Chiricahua	ChW	0
Santa Catalina	Chiricahua	FFL	0
Santa Catalina	Chiricahua	MFL	0
Pinaleño	Sedona	CaL	0
Pinaleño	Sedona	III L	0
Pinaleño	Sedona	V L	0
Pinaleño	Sedona	FemL	0
Pinaleño	Sedona	FemW	0
Pinaleño	Sedona	ChL	0
Pinaleño	Sedona	ChW	0
Pinaleño	Sedona	FFL	0
Pinaleño	Sedona	MFL	0
Pinaleño	Sedona	FFL/CaL	1.63
Pinaleño	Sierra Ancha	ChW	0
Pinaleño	Sierra Ancha	ChL/ChW	0
Pinaleño	Sierra Ancha	MFL/ChW	0
Pinaleño	Chiricahua	CaL	1.18
Pinaleño	Chiricahua	III L	0
Pinaleño	Chiricahua	V L	6.58
Pinaleño	Chiricahua	FemL	0
Pinaleño	Chiricahua	FemW	7.64
Pinaleño	Chiricahua	ChL	0
Pinaleño	Chiricahua	ChW	4.03
Pinaleño	Chiricahua	FFL	0
Pinaleño	Chiricahua	MFL	0
Pinaleño	Chiricahua	FFL/CaL	2.71
Pinaleño	Santa Catalina	CaL	0
Pinaleño	Santa Catalina	III L	0
Pinaleño	Santa Catalina	III W	4.97
Pinaleño	Santa Catalina	V L	0
Pinaleño	Santa Catalina	FemL	0

Oak Creek Canyon cracked rock wall, 35°01′N, 111°44′W, 1707–1981 m, 21.7–25.7 km N Sedona, 35°01′N, 111°44′W, breeding pair, 10 September 1968, M. Cazier et al., 1 male, 1 female (AMNH) & scenic view from rim, ca. 24 km N Sedona, Hwy 89A, 22 August 1995, K.L. Semones & K.J. McWest, 1 male, 4 females, 3 juveniles (AMNH); Manzanita Camp, 35°55′N, 111°44′W, 25 July 1952, M. Cazier, W. Gertsch & R. Schrammel, 1 female (AMNH); Upper Oak Creek Canyon S of Flagstaff, 35°01′N, 111°44′W, 18 August 1949, L.F. Brady, 1 male (AMNH); 9.7 km N Sedona, 35°55′N, 111°44′W, 11 September 1962, V. Roth, 1 female (AMNH); 21.7–25.7 km N Sedona, 1707–1981 m, along grade cuts, 11 males, 4 females (AMNH) &1 female, 32 first instars (AMNH).

Diagnosis.—*Vaejovis lapidicola* (Fig. 7) can be distinguished from *V. paysonensis* by the following male characters (*V. paysonensis* characters follow in parentheses): hemispermatophore trunk width/hook length 1.08–1.25 (0.87–0.93); larger size in most measurements; fixed finger length/carapace length 0.76–0.84 (0.7–0.77); more elongate metasoma segment III with length/width ratio 1.2–1.37 (1.03–1.07). Female metasoma segment III length/width ratio also differs with 1.1–1.26 (1–1.13).

Vaejovis lapidicola can be distinguished from *V. cashi* by the following characters (*V. cashi* characters follow in parentheses): pectinal tooth modes for females 12, range 9–13 (11, range 10–13); modal count for inner accessory denticles of chela movable finger 7 (6), fixed finger 6 (5); metasoma segment III more slender with length/width 1.12–1.26 (0.89–1.07) for females and 1.2–1.37 (0.84–1.09) for males; fixed finger length/carapace length 0.72–0.88 (0.59–0.72) for females and 0.76–0.84 (0.58–0.68) for males; hemispermatophore lamina length/hook length 2.57–2.73 (1.93–2.0) and trunk width/hook length 1.08–1.25 (0.78–1.03).

Vaejovis lapidicola can be distinguished from *V. deboerae* by the following characters (*V. deboerae* characters follow in parentheses): movable finger inner accessory denticle mode 7 (6); subacular tubercles mostly low and subtle, 90% (14%).

Vaejovis lapidicola can be distinguished from *V. vorhiesi* by the characters indicated in the diagnosis for that species.

Distribution.—This species is known from areas around the city of Flagstaff and between Flagstaff and the city of Sedona, Yavapai County and Coconino County, north-central Arizona, USA.

Vaejovis paysonensis Soleglad 1973

Vejovis paysonensis Soleglad 1973:363–371 (original description), figs. 16–22, 24, 26–28.

Vaejovis paysonensis: Kovarík 1998:147; Graham 2006:3, 6; Graham 2007:1, 3, 13; Ayrey 2009:9.

Type material.—Holotype: female, 40.2 km NE of Payson (34°18′N, 111°44′W), Gila County, Arizona, USA (AMNH). Paratypes: 1 male (AMNH; allotype), 7 females, 1 subadult female, 3 subadult males (MES?), same locality as holotype.

Material Examined.—USA: *Arizona*: Gila County: Payson, 34°14′N, 111°19′W, 5–11 May 1969, R. Erno, 2 females (CAS) & 3 May 1969, T. Lutz, 1 female (CAS) & 19 April 1905, W.L. Chapel, 1 female (CAS); 4.8 km N Experimental Station along Globe-Young Rd. at intersection of Armer Mt. Rd., in pine forest with some oak, dark fine soils, 33°50′N, 111°58′W, 1798 m, S.C. Williams, 3 males, 36 females, 6 juveniles (CAS).

Diagnosis.—*Vaejovis paysonensis* (Fig. 7) can be distinguished from *V. cashi* by the following characters (*V. cashi* characters follow in parentheses): pectinal tooth modes for males 12, range 12–13 (13, range 11–16); modal count for

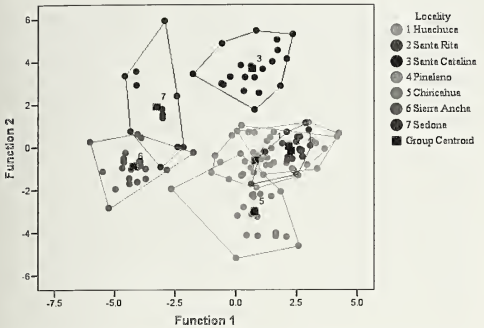


Figure 4.—Plot of all female specimens of montane *Vaejovis* scorpions measured according to the first two functions created from the discriminant function analysis. Function 2 has the highest correlation with all measurements while Function 1 is most highly correlated with metasoma segment III width.

inner accessory denticles of chela movable finger 7 (6), fixed finger 6 (5); subaculear tubercles mostly low and subtle mounds, 72% (0%); hemispermatophore lamina length/hook length 2.27–2.64 (1.93–2.00); male chela wider relative to length with length/width 3.68–3.91 (3.91–4.77).

Vaejovis paysonensis can be distinguished from *V. deboerae* by the following characters (*V. deboerae* characters follow in parentheses): pectinal tooth modes for males 13, range 11–16 (12, range 11–15), for females 11, range 10–12 (13, range 12–14); movable finger inner accessory denticle mode 7 (6); fixed finger length/chela length 0.46–0.50 (0.49–0.62) in females, 1.03–1.07 (1.07–1.25) in males; hemispermatophore lamina length/hook length 2.27–2.64 (2.62–3.28).

Vaejovis paysonensis can be distinguished from *V. vorhiesi* and *V. lapidicola* by the characters indicated in the diagnoses for those species.

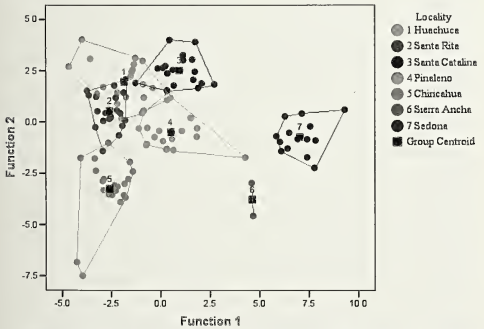


Figure 5.—Plot of all male specimens of montane *Vaejovis* scorpions measured according to the first two functions created from the discriminant function analysis. Function 1 is most highly correlated with chela width. Function 2 is most highly correlated with metasomal segment lengths but is highly correlated with all measurements except chela width.

Table 11.—Classification results for females from the SPSS discriminant function analysis output showing the numbers of specimens from each of seven groups of montane *Vaejovis* scorpions that were misclassified when using the functions that were created from the analysis. Overall, 86.8% of cases were grouped correctly. Groups: 1 = Huachuca, 2 = Santa Rita, 3 = Santa Catalina, 4 = Chiricahua, 5 = Pinaleño, 6 = Sierra Ancha, 7 = Sedona.

	Predicted group membership								
	Group	1	2	3	4	5	6	7	Total
Original count	1	14	2		4				20
	2	4	15		2				21
	3			20					20
	4	1	2		17				20
	5				1	18	1		20
	6						23		23
	7						1	11	12

Distribution.—Near the city of Payson and the Sierra Ancha Mountains, Gila County, central Arizona, USA.

Vaejovis cashi Graham 2007

Vaejovis cashi, Graham 2007:1–3, 6–10, 13 (original description), figs. 15–27; Ayrey 2009:3, 6, 8–10.

Type material.—Holotype: adult female, taken from under stones on the northwest flank of the Chiricahua Mountains, Arizona, USA, 31°55.406′N, 109°15.7057′W; 18 June 2001, D. Vernier (Private collection of M.R. Graham). Paratype: 1 adult female from same locality as holotype.

Material examined.—USA: *Arizona*: Cochise County, Chiricahua Mountains: Ash Spring, 9.7 km SW Portal, 31°51′N, 109°11′W, April 1965, B. & C. Durden, 1 female (AMNH); Rustler Park, 31°54′N, 109°16′W, 2591 m, 25–26 August 1952, B. Malkin, 7 males, 8 females, 5 juveniles (AMNH); 4.8 km SW Portal, 31°52′N, 109°10′W, 1 April 1966, B. Vogel, 1 juvenile (AMNH); 4.8 km S Portal, leaf litter, 31°52′N, 109°10′W, 16 March 1966, B. Vogel, 2 females, 1 juvenile (AMNH); 8 km S Portal, South Fork of Cave Creek, 31°51′N, 109°11′W, 30 May 1976, B. Warner, 7 females (AMNH); Cave Creek Canyon, 8 km W Portal, 31°52′N, 109°11′W, 14 August 1974, M. Cazier, 1 male, 3 females, 13 first instars (AMNH);

Table 12.—Classification results for males from the SPSS discriminant function analysis output showing the number of specimens from each of seven groups of montane *Vaejovis* scorpions that were misclassified when using the functions that were created from the analysis. Overall, 95.7% of cases were grouped correctly. Groups: 1 = Huachuca, 2 = Santa Rita, 3 = Santa Catalina, 4 = Chiricahua, 5 = Pinaleño, 6 = Sierra Ancha, 7 = Sedona.

	Predicted group membership								
	Group	1	2	3	4	5	6	7	Total
Original count	1	17	3						20
	2	1	19						20
	3			18					18
	4				19			1	20
	5					21			21
	6						2		2
	7							15	15

16–19 July 1952, M. Cazier & R. Schrammel, 3 females (AMNH); Roadcuts 19.3–24.1 km W Portal, Onion Saddle, 31°56′N, 109°16′W, 1981–2317 m, 21 July 1969, M. Cazier et al., 10 males, 5 females (AMNH); Rustler Park to 0.8 km N of park, along roadcuts, rock outcrops, cliffs, 31°54′N, 109°16′W, 22 July 1969, M. Cazier et al., 45 males, 12 females, 1 juvenile (AMNH); 8 km W Portal, 31°52′N, 109°11′W, 1829–1981 m, on banks of road cuts, rocky and dead plant material preferred, 14 August 1974, Cazier family, 65 males, 3 females (AMNH); 8 km W Portal, 31°52′N, 109°11′W, 4 July 1956, E. Ordway, 1 female (AMNH); Rustler Park, 31°54′N, 109°16′W, 25 February 1957, E. Ordway, 1 female (AMNH); East Turkey Creek, Coronado National Forest, Portal, 31°51′N, 109°20′W, 1951 m, soil in pinecones, 11 October 1961, E.A. Maynard, 1 male, 1 juvenile (AMNH); Turkey Creek, 31°51′N, 109°20′W, 28 June 1967, Gertsch & Hastings, 1 female (AMNH); Rustlers Camp, 31°54′N, 109°16′W, 1 June 1952, W.J. Gertsch, 2 males, 6 females (AMNH); Barfoot Meadow, 31°55′N, 109°16′W, 8 September 1963, W.J. Gertsch & V. Roth, 2 males, 6 females (AMNH); Barfoot Park, 16.1 km W Portal, 31°55′N, 109°16′W, 19 July 1964, Gertsch & Woods, 1 male, 1 female (AMNH); Barfoot Park, 31°55′N, 109°16′W, 27 June 1967, Gertsch & Hastings, 1 female (AMNH); Barfoot Park, 31°55′N, 109°16′W, 16 August 1964, Hastings, 2 females (AMNH); South Fork Cave Creek, 31°31.8′N, 109°6.5999′W, J. & W. Ivie, 1 male (AMNH); Southwestern Research Station can–traps, 31°52′N, 109°12′W, 29 July 1960, J. Cole, 2 females, 14 first instars (AMNH); Trail to Barfoot Lookout, 31°54′N, 109°16′W, 2597m, 16 July 1961, J. Cole & T. Ryan, 1 male (AMNH); Southwestern Research Station, 8 km W Portal, 31°52′N, 109°12′W, 22 April 1961, J. Rozen & R. Schrammel, 1 female (AMNH); Pinery Canyon, 31°56′N, 109°16′W, 10 May 1956, K. Statham, 1 female (AMNH); Rustlers Camp, 31°54′N, 109°16′W, 1 June 1952, M. Cazier, W. Gertsch & R. Schrammel, 2 males, 7 females (AMNH); Turkey Creek, 31°51′N, 109°20′W, 1829 m, 31 May 1952, M. Cazier, W. Gertsch & R. Schrammel, 2 males, 3 females (AMNH); Rustler Park, 31°54′N, 109°16′W, 22 August 1963, M. Muma, 1 female, 8 first instars (AMNH); Southfork, 31°52′N, 109°11′W, 6–13 May 1956, M. Statham, 1 female (AMNH); Cave Creek Canyon, 31°52′N, 109°11′W, August 1965, B. & C. Durden, 1 female (AMNH) & 0.16 km E Stewart Camp, 3 June 1973, O.F. Francke, 1 male, 7 females (AMNH) & 0.64 km W Stewart Camp, 3 June 1973, O.F. Francke, 1 male, 1 female (AMNH) & 1.13 km W Stewart Camp, 3 June 1973, O.F. Francke, 1 male, 4 females (AMNH) & 0–3.2 km W Sunny Flat Camp, 5 June 1973, O.F. Francke, 3 males, 63 females, 3 juveniles (AMNH) &10.5 km W Portal, 14 June 1973, O.F. Francke, 2 males, 22 females, 1 juvenile (AMNH); East Turkey Creek, 31°51′N, 109°20′W, 2012 m, 3 June 1973, O.F. Francke, 4 males, 2 females (AMNH); Ash Spring, 1.6 km NW Herb Martir Dam, 12.9 km W Portal, 31°51′N, 109°11′W, 31 July 1965, R. Hastings, 1 female (AMNH); East Turkey Creek, 31°51′N, 109°11′W, 1920m, 29 July 1972, R. Zweifel, 1 female (AMNH); 8 km W Portal, on South Fork, 31°51′N, 109°11′W, 17 April 1964, V. Roth, 1 female (AMNH); 12.9 km W Portal, toward falls, 31°50′N, 109°12′W, 8 April 1963, V. Roth, 2 males, 1 female (AMNH); Rustler Park, 17 August 1963, V. Roth, 1 female (AMNH); South Fork, 31°52′N, 109°11′W, 13 July 1963, V. Roth, 1 female (AMNH); 8 km W Portal, South fork of Cave Creek, 31°52′N, 109°11′W, 17–19 April 1961, W.J. Gertsch, 1 male, 4 females (AMNH); 8 km W Portal, Southwestern Research Station, 31°52′N, 109°12′W, 5–15 August 1955, W.J. Gertsch, 1 female (AMNH); 11.3 km W Portal, 31°52′N, 109°11′W, 4 August 1955, W.J. Gertsch, 1 female (AMNH); Barfoot, 31°55′N, 109°16′W, 1 August 1955, W.J. Gertsch, 1 female (AMNH); Barfoot Park, 31°55′N, 109°16′W, 6 July 1962, W.J. Gertsch, 5 males, 11 females (AMNH); Pinery Canyon, 31°56′N, 109°16′W, 8 September 1950, W.J. Gertsch, 1 female (AMNH); South Fork Cave Creek, 11 September 1950, W.J. Gertsch, 3 males, 3 females (AMNH); South Fork Cave Creek, 31°52′N, 109°11′W, 6.4 km W Portal, 9 September 1964, W.J. Gertsch, 2 females (AMNH); Southwestern Research Station, 31°52′N, 109°12′W, August 1960, Zweifel et al., 5 males, 1 juvenile (AMNH).

Diagnosis.—*Vaejovis cashi* (Fig. 7) can be distinguished from *V. deboerae* by the following characters. (*V. deboerae* characters follow in parentheses): pectinal tooth count mode for females 11, range 10–13 (12, range 11–15); chela fixed finger inner accessory denticle mode 6 (5); smaller body size in all measurements; hemispermatophore blade length/hook length 1.93–2.00 (2.62–3.28).

Vaejovis cashi can be distinguished from *V. vorhiesi*, *V. lapidicola*, and *V. paysonenis* by the characters indicated in the diagnoses for those species.

Distribution.—Known from the Chiricahua Mountains in Cochise County, southeastern Arizona, USA.

Vaejovis deboerae Ayrey 2009

Vaejovis deboerae Ayrey 2009:1–10 (original description), figs. 1–4, 6, 8, 10, 11, 14, 15.

Type material.—Holotype: female, Mt. Lemmon, Santa Catalina Mountains, 32°23.21667′N, 110°41.75′W, intersection of Willow Canyon Circle and Catalina Highway, Pima County, Arizona, USA, 2142 m, 25 August 2008, R.F. Ayrey (CAS). Paratypes: 1 male, 2 females, (CAS), same locality as holotype.

Material examined.—USA: *Arizona*: Pima County, Santa Catalina Mountains: 32°26′N, 110°45′W, 12 April 1936, O. Bryant, 1 female (AMNH); 32°26′N, 110°47′W, 1 October 1938, O. Bryant, 2 females (AMNH); 32°26′N, 110°47′W, 25 May 1937, O. Bryant, 1 male, 4 females (AMNH); Rose Lake, 32°23′N, 110°42′W, 6 October 1973, E. Oliver, 1 male (AMNH); Mt. Lemmon, 32°26′N, 110°45′W, 8 March 1968, H.L & L.L. Stahnke, 1 male (CAS); Sabino Canyon, 32°20′N, 110°46′W, 6 June 1952, M. Cazier, W. Gertsch & R. Schrammel, 1 male (AMNH); Summerhaven, 32°26′N, 110°47′W, 6 June 1952, M. Cazier, W. Gertsch & Schrammel, 4 females (AMNH); Summerhaven, 32°26′N, 110°47′W, 22 August 1950, M.A. Cazier, 1 female (AMNH); Tucson, 32°26′N, 110°45′W, O. Bryant, 1 female (AMNH); Mt. Lemmon 19 June 1954, B. & J. Liming, 3 females (CAS) & 2804 m, 15 August 1974, E. Minch, 1 male (AMNH) & 32°24.6375′N, 110°42.8878′W, 2420 m, 15 June 2007, Z. Valois, 1 male, 2 females, 1 subadult female (AMNH/AMNH-ARA 00002515) & Mt. Lemmon, 32°26′N, 110°45′W, 8 March 1968, H.L & L.L. Stahnke, 1 male (CAS) & vicinity of Summerhaven, 32°14.4′N, 110°27′W, 21 May 1963, W.J. Gertsch & W. Ivie, 1

female, 3 subadult females, 2 juveniles (AMNH) & Summerhaven, 32°26′N, 110°45′W, 10 September 1963, W.J. Gertsch & V. Roth, 1 female, 1 subadult female (AMNH); 32°23′N, 110°41′W, on the road to Mt. Lemmon, Molina Basin, 1524–1829m, 19 August 1995, P. Hyden & D. Wagner, 1 male (AMNH); Sabino Canyon, 32°20′N, 110°46′W, 8 June 1955, R.B. & J.M. Selander, 1 female (AMNH); General Hitchcock Tree, 26 August 1951, T. Cohn, 1 female (AMNH); Bear Canyon Campground, 32°22′N, 110°41′W, 1981 m, 24 July 1965, W.J. Gertsch & R. Hastings, 3 males, 2 females (AMNH); 8 km S Oracle, 32°33′N, 110°44′W, 25 July 1949, W.J. & J.W. Gertsch, 1 juvenile (AMNH); Peppersauce Cave Canyon, 32°32′N, 110°43′W, 21 April, 1961, W.J. Gertsch, 4 female (AMNH); Tucson, Upper Bear Canyon, 32°22′N, 110°41′W, 15 June 1973, D. Richman, 1 female (AMNH); Coronado National Forest, Santa Catalina Hwy, on and near Bear Wallow Rd., between mile marker 22 & 23, rocky road cut slopes, 32°24.495′N, 110°43.317′W, 2375 m, Site 13, 22 June 2006, W. Savary, R. Mercurio, 4 males, 10 females (AMNH/AMNH-ARA 0002507); Coronado National Forest, Santa Catalina Hwy, on and near Incinerator Rd., between mile marker 19 & 20, granitic rocky road cut slopes, 32°24.664′N, 110°43.325′W, 2464 m, Site 14, 22 June 2006, W. Savary & R. Mercurio, 6 males, 2 femlaes, 1 subadult female (AMNH/AMNH-ARA 00002506).

Diagnosis.—This species may be distinguished from the other described species in Arizona by the characters given in the diagnoses of those species.

Distribution.—Known from the Santa Catalina Mountains, Pima County, southern Arizona, USA.

Vaejovis electrum sp. nov.
Figs. 6, 7, 8

Type material.—Holotype male, Wet Canyon (32°38′N, 109°48′W), Forest Camp, Graham Mt., Graham County, Arizona, USA, 12–13 September 1952, B. Malkin (AMNH). Paratypes: 2 males, 3 females, from same locality as holotype (AMNH).

Other material examined.—USA: *Arizona*: Graham County, Pinaleño Mountains: Wet Canyon, Forest Camp, Graham Mt., 32°38′N, 109°48′W, 12–13 September 1952, B. Malkin, 3 males, 6 females, (AMNH); 32°38′N, 109°49′W, 2743 m, 10 September 1937, Bryant, 1 male, 1 female (AMNH); 32°38′N, 109°49′W, 15 September 1940, Bryant, 2 males, 2 females, 12 first instars (AMNH); 38°39′N, 109°49′W, 2256 m, 10 September 1937, Bryant, 2 females (AMNH); 38°38′N, 109°49′W, 16 August 1933, Bryant, 1 male (AMNH); 2.6 km S Arcadia Campground, 32°38.167′N, 109°49.453W, 2179 m, 31 May–1 June 2000, W.D. Sissom et al., 1 male (WDS); Mt. Graham, 1.4 km S Arcadia Campground, 32°38.633′N, 109°49.102W, 31 May–1 June 2000, W.D. Sissom et al., 1 male, 3 female (WDS); 6.4 km SW Cottonwood, 8 June 1973, O.F. Francke, 1 male, 1 female (AMNH); Arcadia Campground, 32°38′N, 109°49′W, 4 April 1969, G.J. Doleyard, 2 females (AMNH); Wet Canyon, under rock on south-facing slope, 30 m above stream, 32°38′N, 109°48′W, 1942 m, 15 June 1967, K. Brown, 1 female (AMNH); Turkey Flat, 32°37′N, 109°49′W, 15 September 1973, R. Kempton, 3 males, 2 females, 10 juveniles (AMNH); south of Safford, 2 September 1973, R. Kempton, 1 male, 1 female (AMNH); Pinecrest (also Turkey Flat), 32°37′N, 109°49′W, 13 September 1950, W.J. Gertsch, 3 males, 6 females, 1 juvenile (AMNH); Cluff Dairy turnoff, Swift Trail Rd., deep in Ponderosa pine log on ground, 32°38′N, 109°49′W, 2256 m, 10 July 1966, W.L. Minckley, 4 females (AMNH); Arcadia Campground, 32°38′N, 109°49′W, 31 May 2000, W.D. Sissom et al., 1 male, 16 females (WDS); Hwy. 366 into Coronado National Forest, climbing Mount Graham, just past mile marker 126, 19 km from junction with Hwy. 191, under rocks in pine forest, 32°38.5517′N, 109°49W.1033′, 1684 m, 25 July 2007, J. Huff, 1 male, 3 females, 1 juvenile (AMNH); Hwy. 366 into Coronado National Forest, climbing Mount Graham, "Ladybug Trail No. 329" at mile marker 131, 26.6 km from junction with Hwy. 191, under rocks in pine forest, 32°37.35′N, 109°49.4033′W, 25 July 2007, J. Huff, 1 male, 3 females (AMNH).

Etymology.—Specific epithet is from the Latin word *electrum*, meaning amber in reference to the amber-like coloration of this species, and is used as a noun in apposition.

Diagnosis.—*Vaejovis electrum* can be distinguished from *V. lapidicola* and *V. paysonensis* by 1) having 6 inner accessory denticles on the movable finger instead of 7, and 2) having a smaller chela width. It can be distinguished from *V. vorhiesi* by 1) usually having multiple subaculear tubercles or well-developed subaculear tubercles and rarely having only a subtle, low mound for a tubercle, 2) having lower pectinal tooth counts, mode 13 for males and 12 for females, and 3) having hemispermatophore lamina length/width 3.89–4.63 instead of 2.35–3.09. It can be distinguished from *V. cashi* by 1) having a higher pectinal tooth count mode for females (12 instead of 11), 2) having hemispermatophore lamina length/hook length ratio 2.2–2.8 instead of 1.93–2.0, and 3) by having an overall larger body size, especially in the male. *Vaejovis electrum* can be distinguished from *V. deboerae* by 1) having a mode of 5 inner accessory denticles on the chela fixed finger instead of 6, and 2) having a smaller body size, especially in males, but particularly smaller in carapace length and metasoma segment V length for both sexes. *Vaejovis electrum* can be distinguished from *V. feti*, a New Mexican species, by 1) having greater pectinal tooth count modes (males: 13 instead of 11–12; females: 12 instead of 10), 2) having well-developed subaculear tubercles instead of tubercles being present as only a low mound, and 3) having larger body size.

Description.—The following description is based mostly on the male holotype; female characters, where notably different, are indicated.

Coloration: Base color of body surfaces light yellow-orange to brown (Fig. 7). Carapace with distinct fuscous pattern. Coxosternal region light yellow with no fuscous markings. Pretergites with fuscous posterior margin except fuscosity weak to absent along midline. Post-tergites with little to no markings along midline and possessing lateral fuscous blotches. Sternites yellow with no fuscous markings except for extreme lateral edges. Pectines pale yellow; sternite V with pale yellow patch on posterior margin (absent in females). Metasomal carinae with underlying fuscous markings (except for ventral carinae of metasomal segments I and II). Dorsal surface of metasoma with triangle or arrow-shaped fuscous pattern on segments I–III, longitudinal band of fuscosity on

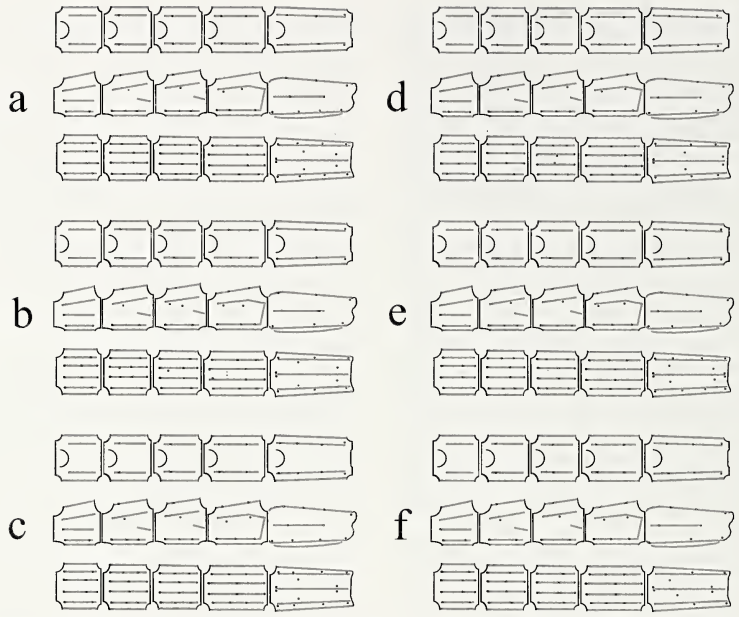


Figure 6.—Setal maps displaying (from top to bottom) a dorsal, lateral and ventral view of the metasoma with plots of the metasomal setae from six species of *Vaejovis* scorpions from different montane locations in Arizona, USA: A. *V. vorhiesi* Stahnke 1940 from the Huachuca Mountains; B. *V. lapidicola* Stahnke 1940 from Flagstaff; C. *V. paysonensis* Soleglad 1973 from the Sierra Ancha Mountains; D. *V. cashi* Graham 2007 from the Chiricahua Mountains; E. *V. deboerae* Ayrey 2009 from the Santa Catalina Mountains; F. *V. electrum* sp. nov. from the Pinaleño Mountains.

IV and two longitudinal lateral bands on V. Ventrolateral and lateral supramedian intercarinal space with fuscous pattern on posterior portion. Telson yellow; aculeus dark brown; ventral median marked by fuscous band. Pedipalps: femur, patella, and chela light yellow with faint dusky markings, especially near base of fingers and along external carinae; denticles of finger yellow-orange to orange-brown. Legs light yellow with some fuscous markings on prolateral surfaces of femur, patella, tibia, and basitarsus with distinct banded pattern on patella; telotarsus yellow.

Prosoma: Carapace slightly longer than posterior width. Anterior margin slightly indented but not bilobed, with six anterior-facing setae. Carapace finely covered with minute granules. Two median eyes present; two rows of three lateral eyes with seta behind each lateral eye row.

Mesosoma: Tergites I–VI: median carina covered by granules and increasingly distinct on each successive segment from weak on I to moderate on VI; submedian carinae indistinct, merged into general granulation associated with the lateral markings. Tergite VII: median carina present as a moderate, granulated hump about two-thirds the length of the post-tergite up from the posterior margin; submedian and lateral carinae strong, irregularly crenulate; submedian carinae originating from about two-thirds the length of the post-tergite up from the posterior margin and extending to the posterior margin; lateral carinae spanning the length of the post-tergite. All tergites possessing granules with larger granules on posterior half of the segment; large granules on lateral surface of VIII. Male genital opercula without median longitudinal membranous connection (in females connected on anterior 4/5), genital papillae well developed (absent in females). Pectinal tooth count 13/13 (12–14 in males, 11–13 in females). Sternites III–VI finely porous, lustrous medially; finely granular and less lustrous laterally; moderately setose throughout. Sternite III with posterior white patch in males. Sternite VII with lateral carinae present as an irregular row of slightly enlarged granules.

Metasoma: (Fig. 8g) Segment I 1.33 times wider than long; II 1.13 times longer than wide, III as long as wide, IV 1.24 times longer than wide, V 1.96 times longer than wide. Segments I–IV: Carination: Dorsolateral carinae on I–IV strong, crenulate to serrate; distal-most denticles on I–IV distinctly enlarged, spinoid. Lateral supramedian carinae on I–IV strong, crenulate; distal-most denticles distinctly enlarged, spinoid on I–III; widely flared on IV. Lateral inframedian carinae on I complete, moderate, granular; on II present on posterior one-half, granular; on III present on posterior one-quarter, granular; on IV absent. Ventrolateral carinae on I–III moderate, granulate to crenulate; on IV moderate, crenulate. Ventral submedian carinae on I weak,

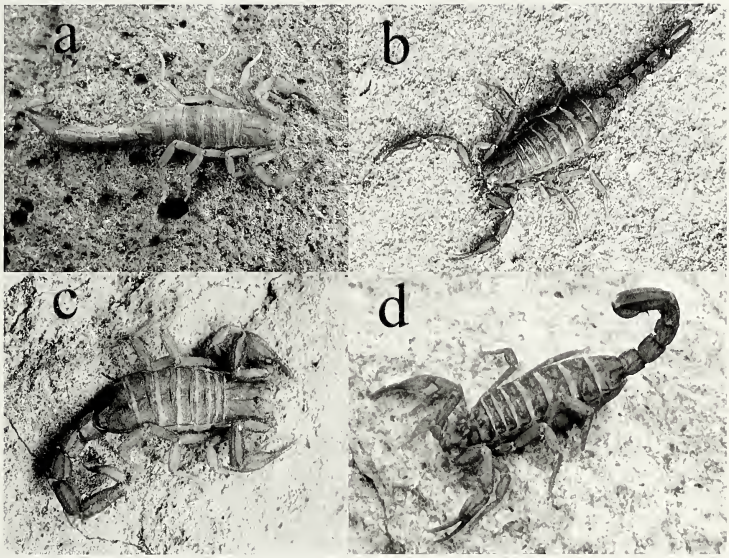


Figure 7.—Live specimens of montane *Vaejovis* scorpions from Arizona: a. *V. lapidicola* Stahnke 1940; b. *V. cashi* Graham 2007; c. *V. paysonensis* Soleglad 1973; d. *V. electrum* sp. nov. All photos courtesy of W.D. Sissom.

granular; on II–IV moderate, crenulate. Dorsal intercarinal spaces on I–IV finely minutely granular, lustrous. Dorsolateral intercarinal spaces on I–IV finely granular, with sparse coarse granulation. Lateral faces mostly with minute granulation and some larger granules interspersed throughout. Ventral spaces finely, minutely granular. Segment I–IV setation: dorsolaterals, 0:1:1:2; lateral supramedians, 0:1:1:2; lateral inframedians, 1:0:0:0; ventrolaterals, 2:2:2:2; ventral submedians, 3:3:3:3; setae of ventromedian intercarinal spaces, 0:0:0:0. Segment V: Dorsolateral carinae moderate, basal one-third serrate, remaining distal portion smooth. Lateromedian carinae present on anterior three-fifths, weak, granular. Ventrolateral and ventromedian carinae strong, serrate. Dorsal proximal transverse furrow strong, smooth, lustrous; longitudinal furrow weak, shallow. Dorsal and lateral intercarinal spaces finely granular; ventral intercarinal spaces, sparsely decorated with course granules. Segment V setation: dorsolaterals, 3; lateromedians, 1; ventrolaterals, 3; ventromedian, 4.

Telson: (Fig. 8g) All surfaces smooth, lustrous. Vesicle with about 18 pairs of setae; aculeus with a few setae on base. Subaculear tubercle well-developed, simple. Aculeus 36% of telson length.

Pedipalp: Femur (Fig. 8e, f) tetracarinate. Prodorsal and proventral carinae strong, crenulate. Retrodorsal carina moderate, irregularly granular. Retroventral carina moderate, smooth to finely granular. Prolateral face with about 8 large granules medially; dorsal, ventral and retrolateral faces finely granular with sparse coarser granulation. Trichobothrial pattern Type C, orthobothriotaxic (Vachon 1974). Setation: prolateral face with 1 supramedial seta, 2 inframedial setae; retrolateral face with 2 medial setae.

Patella: Pentacarinate. Prodorsal carina strong; proventral carinae strong, crenulate. Retrodorsal and retroventral carinae moderate, smooth. Promedial carina moderate, irregularly granular. Dorsal, ventral and retrolateral intercarinal spaces finely granular, prolateral intercarinal space finely to moderately coarsely granular. Trichobothrial pattern Type C, orthobothriotaxic (Vachon 1974). Setation: prolateral face with 2 supramedial setae; 2 inframedial setae.

Chela: (Fig. 8a–d) Essentially acarinate, with positions of keels indicated in cross section by faint, rounded elevations and underlined with fuscous markings; intercarinal spaces finely granular. Dentate margin of fixed finger with primary denticle row divided into six subrows by five larger granules; six inner accessory denticles, with the distal-most paired with the terminal denticle, the next four with enlarged primary row granules. Dentate margin of movable finger with primary denticle row broken up into six subrows by five enlarged denticles; distal-most subrow consisting of a single apical denticle and its enlarged primary row denticle; six inner accessory denticles, with the distal denticle paired with the terminal denticle and the next five paired with enlarged primary row denticles. Chela length/width ratio 4.06; fixed finger length/carapace length ratio, 0.68; fixed finger length 49% of total chela length. Trichobothrial pattern Type C, orthobothriotaxic (Vachon 1974).

Legs: Prolateral surface of patella on legs I–IV bearing a single seta. Proventral margin of patella bearing two setae on I–II, three setae on III–IV. Retroventral margin of patella

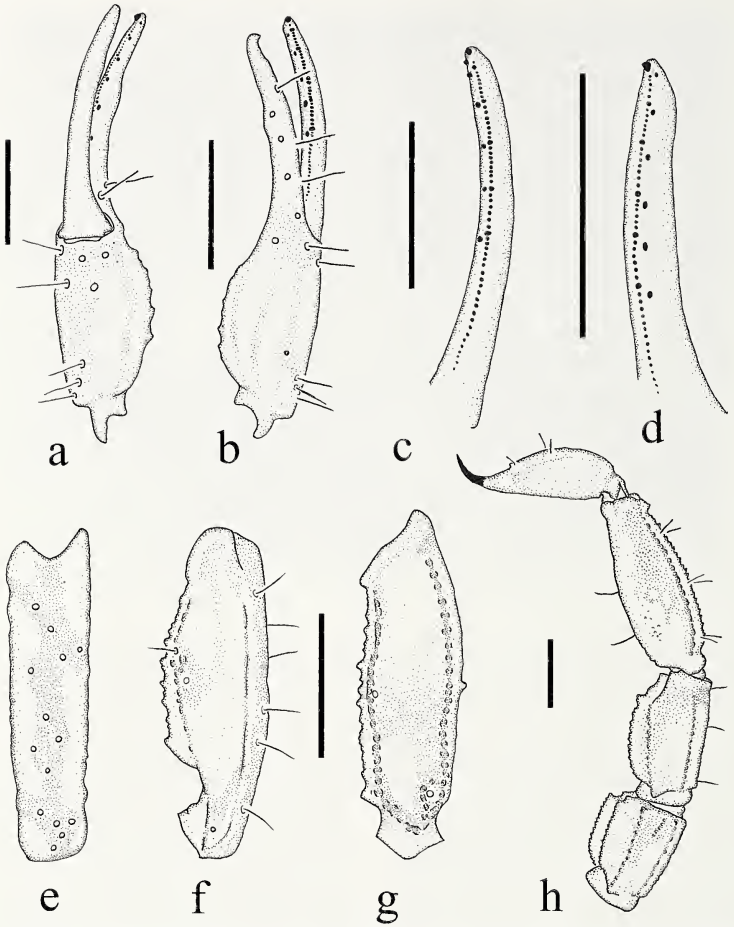


Figure 8.—Illustrations of various features of *Vaejovis electrum* sp. nov. Scale bars to the left of each figure represent 1 mm, except for patellae, which were not measured. Note in A and B that the bulge of inner margin of the fixed finger is an aberration in the type specimen and not an artifact of illustration. a. Ventral aspect of pedipalp chela; b. Dorsal aspect of pedipalp chela; c. Pedipalp chela movable finger; d. Pedipalp chela fixed finger; e. Dorsal aspect of pedipalp femur; f. Dorsal aspect of pedipalp patella; g. External aspect of pedipalp patella; h. Lateral view of metasomal segments III–V and telson.

bearing three setae on I–IV. Basitarsus on legs I–III with two ventrosubmedian and one retrolateral rows of spinules; prolateral ventrosubmedian spinule extending proximally only a short distance from distal-most seta; spinule rows interrupted at irregular intervals by large, stiff setae. Leg IV lacking spinule rows. Telotarsus on all legs with single ventromedian row of spinules.

Hemispermatophore (dissected from topotype male): Measurements (in mm): lamina length 1.17, lamina width 0.30, hook length 0.53, trunk width 0.53. Lamina length/lamina width ratio 3.89, lamina length/hook length ratio 2.19, trunk width/hook length ratio 1.Sperm plug lacking spines.

Measurements of holotype male (in mm): Total length (estimated), 43.00; carapace length, 2.62; metasoma III length 1.46, width 1.46; metasoma V length 2.74, width 1.40; femur length 2.39, width 0.70; chela length 3.78, width 0.93; fixed finger length 1.86; movable finger length 2.33.

Variation.—As with other scorpions in this group, *V. electrum* exhibits sexual dimorphism in morphometrics. Ranges for measurements of males with females in parentheses

(all measurements in mm): carapace length 2.56–3.03 (3.2–3.72); metasoma III length 1.46–1.75 (1.57–2.04), width 1.19–1.60 (1.6–1.93); metasoma V length 2.68–3.18 (3.11–3.72), width 1.16–1.50 (1.51–1.86); femur length 2.24–2.62 (2.74–3.51), width 0.64–0.76 (0.81–0.96); chela length 3.61–4.45 (4.72–5.44), width 0.81–1.03 (1.05–1.28); fixed finger length 1.80–2.21 (2.39–2.79); movable finger length 2.24–2.78 (2.86–3.40). Ratios for males with females in parentheses: chela length/width 4.03–4.71 (3.94–4.72); femur length/width 3.20–3.64 (3.06–3.75); metasoma III length/width 0.98–1.28 (2.32–2.89); metasoma V length/width 1.92–2.43 (1.84–2.22). Other variation can be seen in Tables 1–7.

Distribution.—Known from the Pinaleño Mountains, Graham County, Arizona, USA.

DISCUSSION

Most species descriptions are accompanied by a section detailing the variation in the new species being described and are based on multiple specimens. The ability to distinguish one species from another stems from an understanding of that intraspecific variation. When this variation is not taken into consideration, new species can be described without consistent diagnostic characters that identify that species. For example, a new species may be described and diagnosed from related species by the presence of a few characters found in the holotype and a few other specimens when a larger sample size would have revealed that the characters overlap so greatly as to be useless in diagnosing the species. In such a situation, had a larger sample size been collected and examined for the initial description of the species, it would have been apparent that the character was not useful for distinguishing the species from others.

This scenario has occurred with some of the "*vorhiesi* complex" species from Arizona. The original description of *V. cashi* was based upon only two specimens (Graham 2007). One of the characters Graham (2007) used to distinguish *V. vorhiesi* from *V. cashi* was the number of denticles on the third median subrow of the pedipalp chela movable finger. However, the variability was great in the number of denticles per subrow. Graham (2007) stated that *V. cashi* should have 6 or 7 denticles on the third subrow but in the sample of 10 specimens from the Chiricahua Mountains used in this study, 11 of the 20 movable fingers had 8–9 denticles, which was the range Graham gave for *V. vorhiesi*. It is not surprising that with only two specimens of *V. cashi* the ranges he found were completely non-overlapping.

This also happened with the lateral inframedian carinal differences reported by Ayrey (2009). *Vaejovis deboerae* is reported as having longer carinae on segments II and III of the metasoma. Although the *V. deboerae* specimens I examined may have had a slightly greater proportion of specimens with long lateral inframedian carinae, many of the other species also had specimens with long lateral inframedian carinae. *Vaejovis deboerae* is also supposed to be different from the other species in that segment IV has the lateral inframedian carina present on the distal 2/5 of the segment. The distal end of the segment is where the carina originates, so if a carina is present at all, it is usually found in the distal 2/5 of the segment. Therefore I believe Ayrey was attempting to say that the carina was present on at least the distal 2/5 of the segment. In fact, 29.2% of *Vaejovis deboerae* specimens examined in this study did not have the lateral inframedian carina at all and only 62.5% had the carina present on at least the distal 2/5 of the segment. Additionally, 53.9% of *V. cashi* and 66.2% of *V. electrum* had the carina present on at least the distal 2/5 of metasomal segment IV. That means there is about the same probability to identify a specimen of *V. deboerae* correctly as there is to misidentify *V. cashi* or *V. electrum* specimens as *V. deboerae*.

It must be admitted that the current study also suffers from some low sample sizes. For example, only 2 male specimens of *V. paysonensis* were examined. The rule for reporting measurements with ranges overlapping 10% or less was determined *a priori* to minimize any biases of character reporting. For that reason, measurements of male *V. paysonensis* were included. To exclude them would introduce bias, even though a larger sample size would have been much preferred.

For this study, I used the phylogenetic species concept, which delimits species as the smallest group of individuals that forms a monophyletic group and displays consistent distributions of characters (Donoghue 1985). This species concept has been used in describing scorpion species previously (Prendini 2001). Although many of the traits used to diagnose these species do overlap, the amount of characters, along with the minimal overlap (10% rule), suggest that these species are indeed distinct. Further evidence is found in the discriminant function analysis, especially for males, which misclassified less than 10% of the specimens.

ACKNOWLEDGMENTS

I sincerely thank the following individuals: Dr. W. David Sissom for all of his guidance and advice on distinguishing these species and for obtaining the specimens to examine; Dr. Lorenzo Prendini for his comments regarding species questions in taxonomy; Dr. Richard Kazmaier for his assistance with some of the statistics; Dr. Raymond Matlack for his review of the manuscript; curators Dr. Griswold (CAS) and Dr. Prendini (AMNH) for loaning the material examined and Dr. Sissom for borrowing material on my behalf. This project was supported in part by NSF BIO-DEB 0413453 grant to Dr. Prendini.

LITERATURE CITED

Anderson, R.S. 1993. A 35,000 year vegetation and climate history from Potato Lake, Mogollon Rim, Arizona. Quaternary Research 40:351–359.

Ayrey, R.F. 2009. Sky island *Vaejovis*: a new species (Scorpiones: Vaejovidae). Euscorpius 86:1–12.

Donoghue, M.J. 1985. A critique of the biological species concept and recommendations for a phylogenetic alternative. The Bryologist 88:172–181.

Graham, M.R. 2006. Redescription and lectotype designation of *Vaejovis lapidicola* Stahnke, 1940 (Scorpiones: Vaejovidae). Euscorpius 46:1–6.

Graham, M.R. 2007. Sky island *Vaejovis*: two new species and a redescription of *V. vorhiesi* Stahnke (Scorpiones: Vaejovidae). Euscorpius 51:1–14.

Graham, M.R. & R.W. Bryson. 2010. *Vaejovis montanus* (Scorpiones: Vaejovidae), a new species from the Sierra Madre Occidental in Mexico. Journal of Arachnology 38:285–293.

Kovarík, F. 1998. Stíri [Scorpiones]. Publishing House "Madagaskar", Jihlava, Czech Republic. (in Czech).

Maddison, W. & M. McMahon. 2000. Divergence and reticulation among montane populations of a jumping spider (*Habronattus pugillis* Griswold). Systematic Biology 49:400–421.

McWest, K.J. 2009. Tarsal spinules and setae of vaejovid scorpions (Scorpiones: Vaejovidae). Zootaxa 2001:1–126.

Prendini, L. 2001. A review of synonyms and subspecies in the genus *Opistophthalmus* C.L. Koch (Scorpiones: Scorpionidae). African Entomology 9:17–48.

Prendini, L. 2001. Substratum specialization and speciation in southern African scorpions: the Effect Hypothesis revisited Pp. 113–138. *In* Scorpions 2001: In Memoriam Gary A. Polis. (V. Fet & P.A. Selden, eds.). British Arachnological Society, Burnham Beeches, Buckinghamshire, United Kingdom.

Santibáñez-López, C.E. & O.F. Francke. 2010. New and poorly known species of the *mexicanus* group of the genus *Vaejovis* (Scorpiones: Vaejovidae) from Oaxaca, Mexico. Journal of Arachnology 38:555–571.

Sissom, W.D. & O.F. Francke. 1981. Scorpions of the genus *Paruroctonus* from New Mexico and Texas (Scorpiones, Vaejovidae). Journal of Arachnology 9:93–108.

Sissom, W.D. 1989. Redescription of *Vaejovis occidentalis* Hoffmann with a revised diagnosis for *Vaejovis subcristatus* Pocock (Scorpiones, *Vaejovidae*). Revue Arachnologique 8:179–187.

Sissom, W.D., G.A. Polis & D.D. Watt. 1990. Field and laboratory methods. Pp. 445–461. *In* The Biology of Scorpions. (G.A. Polis, ed.). Stanford University Press, Stanford, California.

Sissom, W.D. 1991. The genus *Vaejovis* in Sonora, Mexico (Scorpiones, Vaejovidae). Insecta Mundi 5:215–225.

Sissom, W.D. 1997. The scorpion fauna of New Mexico, U.S.A. American Arachnology 54:13.

Sissom, W.D. 2000. Family Vaejovidae Pp. 503–553. *In* Catalog of the Scorpions of the World (1758–1998). (V. Fet, W.D. Sissom, G. Lowe & M.E. Braunwalder, eds.). New York Entomological Society, New York.

Soleglad, M.E. 1973. Scorpions of the *mexicanus* group of the genus *Vejovis* (Scorpionida, Vejovidae). Wasmann Journal of Biology 31:351–372.

Stahnke, H.L. 1939. The scorpions of Arizona. Unpublished Ph.D. Dissertation, Iowa State University, Ames, Iowa.

Stahnke, H.L. 1940. The scorpions of Arizona. Iowa State College Journal of Science 15:101–103.

Stahnke, H.L. 1974. Revision and keys to the higher categories of Vejovidae. Journal of Arachnology 1:108–141.

Vachon, M. 1974. Étude des caráctères utilisés pour classer les familles et les genres de Scorpions (Arachnides). I, Les trichobothriaux et types de trichobothriotaxie chez les scorpions. Bulletin du Muséum National d'Histoire Naturelle, Paris, 3e Séries 140:857–958.

Warshall, P. 1995. The Madrean sky island archipelago: A planetary overview Pp. 6–18. *In* Biodiversity and Management of the Madrean Archipelago: The Sky Islands of the Southwestern United States and Northwestern Mexico. (L. DeBano, P.F. Ffolliott, A. Ortega-Rubio, G.J. Gottfried, R.H. Hamre & C.B. Edminster, eds.). General Technical Report RM-GTR-264, U.S. Department of Agriculture, Fort Collins, Colorado.

Yahia, N. & W.D. Sissom. 1996. Studies on the systematics and distribution of the scorpion *Vaejovis bilineatus* Pocock (Vaejovidae). Journal of Arachnology 24:81–88.

Manuscript received 27 January 2011, revised 10 August 2011.

2011. The Journal of Arachnology 39:439–443

Olfaction-based mate-odor identification by jumping spiders from the genus *Portia*

Robert R. Jackson and **Fiona R. Cross**: School of Biological Sciences, University of Canterbury, Private Bag 4800, Christchurch, New Zealand; International Centre of Insect Physiology and Ecology (ICIPE), Thomas Odhiambo Campus, P.O. Box 30, Mbita Point, Kenya. E-mail: robert.jackson@canterbury.ac.nz

Abstract. Jumping spiders (Salticidae) are known for having good eyesight, but the extent to which they also rely on olfaction is poorly understood. We report here new information on the olfactory abilities of the salticid genus *Portia*. We investigated for the first time the ability of adult males and females of four *Portia* species (*P. africana*, *P. schultzi*, *P. fimbriata* and *P. labiata*) to discriminate between mate and non-mate odor. In a Y-shape olfactometer, males of all four species chose the odor from an opposite-sex conspecific significantly more often than they chose a no-odor control, but the number of males that chose the odor from an opposite-sex heterospecific or the odor from a same-sex conspecific was not significantly different from the number of males that chose the control. The number of female test spiders that chose the odor from an opposite-sex conspecific or the odor from a same-sex conspecific was not significantly different from the number of females that chose the control. The implications of these findings for understanding *Portia*'s mating system are discussed.

Keywords: Olfaction, mate-identification, mating systems, pheromones, Salticidae

Jumping spiders (Araneae: Salticidae) are renowned for having unique, complex eyes (Land & Nilsson 2002), eyesight based on exceptional spatial acuity and intricate vision-based behavior. Yet chemoreception also plays an important role in salticid predatory and mating behavior, either in conjunction with or as alternatives to vision-based signals (Pollard et al. 1987; Clark et al. 2000; Jackson et al. 2002, 2005). In particular, it may be common for salticid males to gain information about the presence of potential mates by detecting chemical traces (i.e., chemical signpost signals) left behind on draglines or nest silk (Jackson 1987; Clark & Jackson 1994a, b; 1995a, b; Taylor 1998; Clark et al. 1999). Considerably less is known about the extent to which salticid mating strategies depend on the detection and identification of volatile compounds (i.e., olfaction), with most of what we currently know having come from a single species, *Evarcha culicivora* Wesolowska & Jackson 2003. This unusual salticid from East Africa feeds indirectly on blood by targeting blood-carrying mosquitoes as preferred prey (Cross & Jackson 2010a), and experiments have shown that *E. culicivora* can identify this prey even when restricted to using sight alone or olfaction alone (Jackson et al. 2005). Human odor and the odor of particular plant species are also salient to this spider (Cross & Jackson 2009a, 2011b). Moreover, even when restricted to using olfaction alone, each sex of *E. culicivora* can identify potential mates (Cross & Jackson 2009b, c) and also determine whether a potential mate has recently fed on a blood-carrying mosquito or whether it has fed on something else (Cross et al. 2009).

Here we report on an experimental study of olfaction-based mate-identification behavior by *Portia africana* (Simon 1886), *Portia schultzi* Karsch 1878, *Portia fimbriata* (Doleschall 1859) and *Portia labiata* (Thorell 1887), species that are only distantly related to *E. culicivora*. Salticid systematics remains poorly understood, but three major taxa are generally recognized, the Salticoida, Spartaeinae and Lyssomaninae (Maddison & Hedin 2003). *E. culicivora*, along with most salticids, is a salticoid. *Portia* belongs to the subfamily Spartaeinae, and spartaeines are known for having unusual predatory strategies (Su et al. 2007). Although most salticids probably prey primarily on insects (Richman & Jackson 1992), most spartaeines that have been studied specialize at feeding on other spiders (i.e., they are 'araneophagic'). Part of what 'araneophagy' means is that these salticids adopt prey-specific tactics for capturing other spiders, and also that they express a strong, active preference for eating other spiders (Jackson & Pollard 1996; Li & Jackson 1996; Nelson & Jackson 2011). For an araneophagic salticid, making use of olfactory cues from prey may often be especially advantageous because another spider is not only potential prey but also a potential predator. Earlier research has provided experimental evidence of olfactory prey identification by two araneophagic spartaeines, *Portia fimbriata* (Jackson et al. 2002) and *Cyrba algerina* (Lucas 1846) (Cerveira & Jackson 2011).

Owing to how encounters between opposite-sex conspecifics can end in cannibalism, the prey-choice and mate-choice decisions of salticids may often be intertwined (Elgar 1992; Jackson & Pollard 1997). The overlap between predatory and mating strategies may be especially evident when we consider *Portia* and other araneophagic salticids. Encountering *Portia* females may be especially dangerous for *Portia* males (Jackson & Hallas 1986), a risk made all the worse by how with *Portia*, as is commonly the case in animals (Trivers 1972), males are more active than females in initiating courtship. Taken together, this suggests that *Portia* is a salticid in which, for males, early identification of conspecific females would be especially advantageous.

From earlier work on two *Portia* species (*P. africana* and *P. fimbriata*), there is indirect evidence that males, but not females, identify the odor of potential mates (Willey & Jackson 1993; Cross et al. 2007a; Cross & Jackson 2009b). Here we investigate directly for the first time the hypotheses that spiders from the genus *Portia* can identify the odor of potential mates on the basis of olfaction alone and that this is an ability expressed strongly by males but only weakly, if at all, by females.

METHODS

All test spiders were taken from laboratory cultures (second and third generation). The origins of these cultures were Mbita Point (Kenya) for *P. africana*, Malindi (Kenya) for *P. schultzi*, Cairns (Australia) for *P. fimbriata* and Los Baños (Philippines) for *P. labiata*. Voucher specimens were deposited at the National Museums of Kenya (Nairobi), the Museum of Natural History (Wroclaw University, Poland) and the Florida State Collection of Arthropods (Gainesville, Florida).

Standard spider-laboratory rearing and testing procedures were adopted (for details, see Jackson & Hallas 1986). No test spider had prior experience with other *Portia* individuals. For standardization, all test and source spiders were unmated adults that had matured 2–3 wk before testing and all were of a standard body length (accurate to nearest 0.5 mm): males 8 mm, females 10 mm. Hunger level was also standardized, with each test and each source spider fasting for

four days prior to testing. Testing was carried out between 0900 and 1200 h (laboratory photoperiod 12L:12D, lights on 0800 h).

Testing was carried out using a Y-shaped olfactometer (Fig. 1) with air pushed by a pump independently into two chambers, an experimental chamber and a control chamber. Airflow was adjusted to 1500 ml/min using Matheson FM-1000 flow meters, and there was no evidence that this airflow setting impaired locomotion or had any adverse effects on the test spider's behavior. Each chamber was a glass cube made from 5-mm thick glass (inner dimensions, 70 × 70 × 70 mm), with a removable lid. There were two holes (20 mm diam.) situated opposite each other on the cube, each hole being plugged with a rubber stopper. There was a hole in each stopper through which a glass tube (45 mm length, 4 mm diam.) passed, enabling air to move in and out of the chambers. On the stopper, a nylon-netting screen ensured that the test spider could not enter the chamber. New netting was used for each test. From the chambers, air moved independently into the two arms of the Y (the control and the experimental arm).

The odor source (a spider) was in the experimental chamber. There was no odor source in the control chamber. A series of experiments was carried out with each of the four *Portia* species: male tested with conspecific female odor, male tested with heterospecific female odor, male tested with conspecific male odor, female tested with conspecific male odor, female tested with conspecific female odor (see Table 1). Testing *Portia* females with the odor of heterospecific males might have also been of interest, but this would have meant addressing questions somewhat tangential to our specific objective in this study of investigating *Portia*'s ability to discriminate between mate and non-mate odor. We found that the odor of opposite-sex conspecifics was salient to males but not to females (see Results), and this gave us a clear rationale for testing whether *Portia* males had specifically responded to mate odor or whether they had responded to the odor of opposite-sex salticids in general. However, there was no comparable rationale for also investigating this for *Portia* females.

A test spider was confined to a holding chamber at the far end of the test arm for 2 min before testing began. A removable metal grill fit into a slit in the chamber roof, blocking access to the rest of the olfactometer. The grill was lifted to start a test. Once the spider left the holding chamber, it was given 30 min in which to make a choice, with the operational definition of 'choosing' being that it entered either the control arm or the experimental arm of the olfactometer and remained there for 30 s. Each spider usually walked about actively in the olfactometer and we recorded which of the two arms it chose. As a precaution against the possibility that test spider behavior was influenced by traces left by spiders that had been tested previously, the olfactometer was dismantled and cleaned with 80% ethanol and then with distilled water between tests.

Data for each experiment were analyzed using chi-square tests for goodness of fit (null hypothesis: probability of making one of the two choices same as probability of making other choice). Using chi-square tests of independence (null hypothesis: choices made by one group of test spiders same as choices made by other group of test spiders), comparisons were also made between different groups of test spiders. Bonferroni adjustments were applied whenever there was repeated testing of the same data sets (alpha 0.05, adjusted alpha 0.013: see Howell 2002). For data analysis, individuals that failed to choose were ignored. For each experiment, $n = 30$.

RESULTS

For each of the four *Portia* species, the number of males that chose the odor of conspecific females was significantly more than the number of males that chose the no-odor control (Tables 1 & 2). The number of females that chose the odor of conspecific males was not significantly different from the number of females that chose the control. In all other experiments, there was no significant difference between the number of test spiders (male or female) that chose the experimental odor and the number that chose the control.

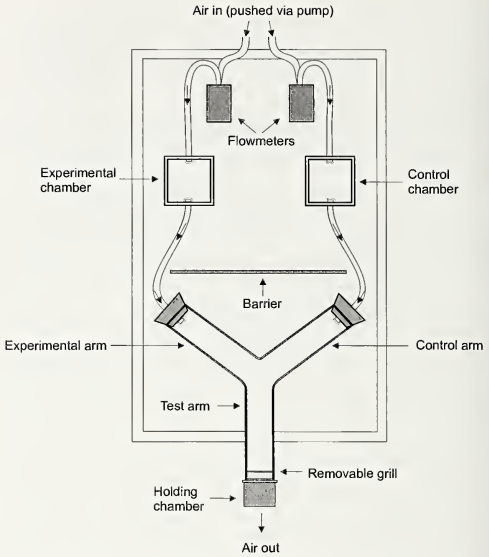


Figure 1.—Olfactometer (not drawn to scale). Arrows indicate direction of airflow. Holding chamber (location of test spider at start of test): 25 mm length, 25 mm inner diam. Start of test: test spider in holding chamber; grill removed, giving access to test arm, control arm and experimental arm. Dimensions of test arm, control arm and experimental arm: 90 mm length, 20 mm inner diam. Opaque barriers prevent test spider from seeing odor source.

Males made significantly different choices when the experimental odor was from an opposite-sex conspecific instead of an opposite-sex heterospecific (*P. africana*: $X^2 = 9.32$, $P = 0.002$; *P. schultzi*: $X^2 = 13.61$, $P < 0.001$; *P. fimbriata*: $X^2 = 8.52$, $P = 0.004$; *P. labiata*: $X^2 = 20$, $P < 0.001$) and they made significantly different choices when the experimental odor was from an opposite-sex conspecific instead of a same-sex conspecific (*P. africana*: $X^2 = 19.20$, $P < 0.001$; *P. schultzi*: $X^2 = 13.61$, $P < 0.001$; *P. fimbriata*: $X^2 = 13.02$, $P < 0.001$; *P. labiata*: $X^2 = 23.72$, $P < 0.001$). Choices made by males were also significantly different from choices made by females when the experimental odor was from an opposite-sex conspecific (*P. africana*: $X^2 = 13.87$, $P < 0.001$; *P. schultzi*: $X^2 = 10.33$, $P = 0.001$; *P. fimbriata*: $X^2 = 11.43$, $P < 0.001$; *P. labiata*: $X^2 = 20$, $P < 0.001$). Choices made by females when the experimental odor was from an opposite-sex conspecific instead of a same-sex conspecific were not significantly different (*P. africana*: $X^2 = 0.27$, $P = 0.605$; *P. schultzi*: $X^2 = 0.07$, $P = 0.793$; *P. fimbriata*: $X^2 = 0.07$, $P = 0.796$; *P. labiata*: $X^2 = 0$, $P = 1.00$).

DISCUSSION

There is abundant evidence that dragline-associated chemical cues assist salticids with the task of identifying potential mates (e.g., Pollard et al. 1987; Clark & Jackson 1995b; Taylor 1998). However, until now, the only direct evidence of olfactory mate identification by salticids has come from *Evarcha culicivora* (Cross & Jackson 2009c; Cross et al. 2009). Both sexes of *E. culicivora* expressed olfactory mate identification. The results of our present study are different because we found evidence for *Portia* males, but not for *Portia* females, of olfaetory mate identification.

Table 1.—Summary of findings from experiments testing four *Portia* species for ability to discern mate odor. Sample size 30 for each species in each cell. (1) For each species, the number of individuals that chose the odor was significantly different from the number that chose the no-odor control. (2) For each species, the number of individuals that chose the odor was not significantly different from the number that chose the no-odor control. (3) Not tested.

	Odor of opposite-sex conspecific	Odor of same-sex conspecific	Odor of opposite-sex heterospecific
Male test spider	(1)	(2)	(2)
Female test spider	(2)	(2)	(3)

Previous work has shown that one of the salticid species we investigated here, *Portia fimbriata*, makes use of olfaction in the context of predation (Jackson et al. 2002). Previous work has also shown that males, but not females, of *P. fimbriata* and *P. africana* escalate conflicts with same-sex rivals when the odor they detect comes from opposite-sex conspecifics instead of from opposite-sex heterospecifics (Cross et al. 2007a; Cross & Jackson 2009b). More specifically, it has been shown that, for these two species, competition for access to mates becomes more intensive for males than for females when odor from opposite-sex conspecifics is present. This is consistent with a simplistic interpretation of Trivers' (1972) argument that sex roles are qualitatively different, with only one sex (usually the male) doing the active courting and competing for access to mates and with only one sex (usually the female) being especially choosy. Recent work with a population of *P. fimbriata* from Queensland (Australia) has shown that males and females of this species may place different emphasis on different resources, with access to potential mates being more important for males (Cross & Jaekson 2009b) and with access to a particular prey species (*Jacksonoides queenslandicus* Wanless 1988, a common salticid species in *P. fimbriata*'s habitat) being more important for females (Cross & Jackson 2011a).

Whether mate odor is salient to salticid females may depend, in part, on the mating system of the species in question. For example, *E. culicivora*'s mating system differs from that of the four *Portia* species we tested, as *E. culicivora* is a salticid species in which mutual mate choice is expressed especially strongly (Cross et al. 2007b). Besides mate odor being salient to males and to females of this species (Cross & Jackson 2009c), both sexes also escalate conflict with a same-sex rival when they are presented with the odor of a potential mate (Cross & Jackson 2009b).

Although we demonstrated olfactory mate identification for males but not for females in the present study, non-significant findings do not, of course, simply prove that *Portia* females are indifferent to male odor. Perhaps the female's response to male odor drops to a level below the sensitivity of our choice-test design. Maybe another experimental design would be more effective. However, regardless of how these non-significant findings are interpreted, our findings imply an interesting male-female difference. Early detection of odor from a potential mate seems to be of greater importance to the males than to the females of *Portia*. This in turn suggests that females are more important as a resource to males (i.e., as potential mates) than males are as a resource to females. However, *Portia* females may also be more dangerous to males (i.e., as potential predators) than males are to females (Jackson & Hallas 1986), and this might in turn make early detection of mate odor more important for males than for females. Being prepared for encounters with a conspecific female may have an especially important self-defense role for males.

Yet caution is needed when basing conclusions on olfactometer data. The basic conclusion implied by our findings is that the odor of conspecific females is salient to *Portia* males. It may be tempting to conclude that *Portia* males are also attracted to female odor, but the biologically relevant effects of female odor on males may be considerably different. The hypothesis we are currently investigating for *Portia* is that, when the odor of a conspecific female is detected, a primary effect on the male is the triggering of selective visual attention (i.e., he becomes prepared to see a conspecific female). There is evidence that prior exposure to the odor of a specific prey (*Jacksonoides queenslandicus*) prepares *P. fimbriata* to see this particular prey species (Jackson et al. 2002). Experiments have also

Table 2.—Choices made by adult males and females of four *Portia* species in Y-shaped olfactometer. Odor source in experimental chamber: adult source spider. Control chamber: no odor source present. $n = 30$ for each row. Choice defined by arm of olfactometer entered and remained in for minimum of 30 s.

Test spider	Source spider	Chose experimental	Chose control	Test for goodness of fit	
				χ^2	P
Portia africana male	*Portia africana* female	28	2	22.533	< 0.001
Portia africana male	*Portia schultzi* female	18	12	1.200	0.273
Portia africana male	*Portia africana* male	12	18	1.200	0.273
Portia africana female	*Portia africana* male	15	15	0.000	1.000
Portia africana female	*Portia africana* female	13	17	0.533	0.465
Portia schultzi male	*Portia schultzi* female	25	5	13.333	< 0.001
Portia schultzi male	*Portia africana* female	11	19	2.133	0.144
Portia schultzi male	*Portia schultzi* male	11	19	2.133	0.144
Portia schultzi female	*Portia schultzi* male	13	17	0.533	0.465
Portia schultzi female	*Portia schultzi* female	12	18	1.200	0.273
Portia fimbriata male	*Portia fimbriata* female	27	3	19.200	< 0.001
Portia fimbriata male	*Portia labiata* female	17	13	0.533	0.465
Portia fimbriata male	*Portia fimbriata* male	14	16	0.133	0.715
Portia fimbriata female	*Portia fimbriata* male	15	15	0.000	1.000
Portia fimbriata female	*Portia fimbriata* female	14	16	0.133	0.715
Portia labiata male	*Portia labiata* female	30	0	30.000	< 0.001
Portia labiata male	*Portia fimbriata* female	15	15	0.000	1.000
Portia labiata male	*Portia labiata* male	13	17	0.533	0.465
Portia labiata female	*Portia labiata* male	15	15	0.000	1.000
Portia labiata female	*Portia labiata* female	15	15	0.000	1.000

shown that the odor of preferred prey (i.e., blood-carrying female mosquitoes) makes *E. culicivora* selectively attentive to the odor and appearance of this particular prey, and that the odor of a potential mate makes *E. culicivora* selectively attentive to the odor of potential mates (Cross & Jackson 2009d, 2010b). We are currently investigating whether the odor of conspecific females also influences selective visual attention by *Portia* males to the appearance of conspecific females.

ACKNOWLEDGMENTS

We thank Godfrey Otieno Sune, Stephen Abok Aluoch and Jane Atieno Obonyo for their assistance at ICIPE. We also gratefully acknowledge support of grants from the Foundation of Research, Science and Technology (UOCX0903), the Royal Society of New Zealand (Marsden Fund (M1096, M1079) and James Cook Fellowship (E5097)), the National Geographic Society (8676-09, 6705-00) and the US National Institutes of Health (R01-AI077722).

LITERATURE CITED

Cerveira, A.M. & R.R. Jackson. 2011. Interpopulation variation in oecobiid-specific prey-capture behaviour and kairomone use by *Cyrba algerina*, an araneophagic jumping spider from Portugal. Journal of Ethology 29:121–129.

Clark, R.J. & R.R. Jackson. 1994a. *Portia labiata*, a cannibalistic jumping spider, discriminates between own and foreign eggsacs. International Journal of Comparative Psychology 7:38–43.

Clark, R.J. & R.R. Jackson. 1994b. Self recognition in a jumping spider: *Portia labiata* females discriminate between their own draglines and those of conspecifics. Ethology, Ecology & Evolution 6:371–375.

Clark, R.J. & R.R. Jackson. 1995a. Araneophagic jumping spiders discriminate between the draglines of familiar and unfamiliar conspecifics. Ethology, Ecology & Evolution 7:185–190.

Clark, R.J. & R.R. Jackson. 1995b. Dragline-mediated sex recognition in two species of jumping spiders (Araneae, Salticidae), *Portia labiata* and *P. fimbriata*. Ethology, Ecology & Evolution 7: 73–77.

Clark, R.J., R.R. Jackson & B. Cutler. 2000. Chemical cues from ants influence predatory behavior in *Habrocestum pulex*, an ant-eating jumping spider (Araneae, Salticidae). Journal of Arachnology 28:309–318.

Clark, R.J., R.R. Jackson & J.R. Waas. 1999. Draglines and assessment of fighting ability in cannibalistic jumping spiders. Journal of Insect Behavior 12:753–766.

Cross, F.R. & R.R. Jackson. 2009a. Odour-mediated response to plants by *Evarcha culicivora*, a blood-feeding jumping spider from East Africa. New Zealand Journal of Zoology 36:75–80.

Cross, F.R. & R.R. Jackson. 2009b. How cross-modality effects during intraspecific interactions of jumping spiders differ depending on whether a female-choice or mutual-choice mating system is adopted. Behavioural Processes 80:162–168.

Cross, F.R. & R.R. Jackson. 2009c. Mate-odour identification by both sexes of *Evarcha culicivora*, an East African jumping spider. Behavioural Processes 81:74–79.

Cross, F.R. & R.R. Jackson. 2009d. Cross-modality priming of visual and olfactory selective attention by a spider that feeds indirectly on vertebrate blood. Journal of Experimental Biology 212: 1869–1875.

Cross, F.R. & R.R. Jackson. 2010a. Mosquito-specialist spiders. Current Biology 20:R622–R624.

Cross, F.R. & R.R. Jackson. 2010b. Olfactory search-image use by a mosquito-eating predator. Proceedings of the Royal Society of London Series B 277:3173–3178.

Cross, F.R. & R.R. Jackson. 2011a. Effects of prey-spider odour on intraspecific interactions of araneophagic jumping spiders. Journal of Ethology 29:321–327.

Cross, F.R. & R.R. Jackson. 2011b. Olfaction-based anthropophily in a mosquito-specialist predator. Biology Letters 7:510–512.

Cross, F.R., R.R. Jackson, S.D. Pollard & M.W. Walker. 2007a. Cross-modality effects during male-male interactions of jumping spiders. Behavioural Processes 75:290–296.

Cross, F.R., R.R. Jackson & S.D. Pollard. 2007b. Male and female mate-choice decisions by *Evarcha culicivora*, an East African jumping spider. Ethology 113:901–908.

Cross, F.R., R.R. Jackson & S.D. Pollard. 2009. How blood-derived odor influences mate-choice decisions by a mosquito-eating predator. Proceedings of the National Academy of Sciences USA 106:19416–19419.

Elgar, M.A. 1992. Sexual cannibalism in spiders and other invertebrates. Pp. 128–155. *In* Cannibalism: Ecology and Evolution Among Diverse Taxa. (M.A. Elgar & B.J. Crespi, eds.). Oxford University Press, Oxford, UK.

Howell, D.C. 2002. Statistical Methods for Psychology, 5th edition. Wadsworth, Belmont, California.

Jackson, R.R. 1987. Comparative study of releaser pheromones associated with the silk of jumping spiders (Araneae, Salticidae). New Zealand Journal of Zoology 14:1–10.

Jackson, R.R., R.J. Clark & D.P. Harland. 2002. Behavioural and cognitive influences of kairomones on an araneophagic jumping spider. Behaviour 139:749–775.

Jackson, R.R. & S.E.A. Hallas. 1986. Comparative biology of *Portia africana*, *P. albimana*, *P. fimbriata*, *P. labiata* and *P. schultzi*, araneophagic, web-building jumping spiders (Araneae: Salticidae): utilisation of webs, predatory versatility, and intraspecific interactions. New Zealand Journal of Zoology 13:423–489.

Jackson, R.R., X.J. Nelson & G.O. Sune. 2005. A spider that feeds indirectly on vertebrate blood by choosing female mosquitoes as prey. Proceedings of the National Academy of Sciences USA 102:15155–15160.

Jackson, R.R. & S.D. Pollard. 1996. Predatory behavior of jumping spiders. Annual Review of Entomology 41:287–308.

Jackson, R.R. & S.D. Pollard. 1997. Jumping spider mating strategies: sex among cannibals in and out of webs. Pp. 340–351. *In* Mating Systems in Insects and Arachnids. (J. Choe & B. Crespi, eds.). Cambridge University Press, Cambridge, UK.

Land, M.F. & D.-E. Nilsson. 2002. Animal Eyes. Oxford University Press, Oxford, UK.

Li, D. & R.R. Jackson. 1996. Prey-specific capture behaviour and prey-preferences of myrmecophagic and araneophagic jumping spiders (Araneae: Salticidae). Revue Suisse de Zoologie hors serie: 423–436.

Maddison, W.P. & M.C. Hedin. 2003. Jumping spider phylogeny (Araneae: Salticidae). Invertebrate Systematics 17:529–549.

Nelson, X.J. & R.R. Jackson. 2011. Flexibility in the foraging strategies of spiders. Pp. 31–56. *In* Spider Behaviour: Flexibility and Versatility. (M.E. Herberstein, ed.). Cambridge University Press, Cambridge, UK.

Pollard, S.D., A.M. Macnab & R.R. Jackson. 1987. Communication with chemicals: pheromones and spiders. Pp. 133–141. *In* Ecophysiology of Spiders. (W. Nentwig, ed.). Springer-Verlag, Heidelberg.

Richman, D. & R.R. Jackson. 1992. A review of the ethology of jumping spiders (Araneae, Salticidae). Bulletin of the British Arachnological Society 9:33–37.

Su, K.F.Y., R. Meier, R.R. Jackson, D.P. Harland & D. Li. 2007. Convergent evolution of eye ultrastructure and divergent evolution of vision-mediated predatory behaviour in jumping spiders. Journal of Evolutionary Biology 20:1478–1489.

Taylor, P.W. 1998. Dragline-mediated mate-searching in *Trite planiceps* (Araneae, Salticidae). Journal of Arachnology 26:330–334.

Trivers, R.L. 1972. Parental investment and sexual selection. Pp. 136–179. *In* Sexual Selection and the Descent of Man. (B. Campbell, ed.). Aldine, Chicago, Illinois.

Wanless, F.R. 1988. A revision of the spider group Astieae (Araneae: Salticidae) in the Australasian region. New Zealand Journal of Zoology 15:81–172.

Wesolowska, W. & R.R. Jackson. 2003. *Evarcha culicivora* sp. nov., a mosquito-eating jumping spider from East Africa (Araneae: Salticidae). Annales Zoologici 53:335–338.

Willey, M.B. & R.R. Jackson. 1993. Olfactory cues from conspecifics inhibit the web-invasion behaviour of *Portia*, a web-invading, araneophagic jumping spider (Araneae, Salticidae). Canadian Journal of Zoology 71:1415–1420.

Manuscript received 1 April 2011, revised 26 August 2011.

2011. The Journal of Arachnology 39:444–448

Male mate choice in *Allocosa alticeps* (Araneae: Lycosidae), a sand-dwelling spider with sex role reversal

Anita Aisenberg[1] and **Macarena González**[1,2]: [1]Laboratorio de Etología, Ecología y Evolución, Instituto de Investigaciones Biológicas Clemente Estable, Av. Italia 3318 CP 11600, Montevideo, Uruguay; [2]CONICET – Laboratorio de Biología Reproductiva y Evolución, F.C.E.F.N., UNC, V. Sarsfield 299, Córdoba, Argentina. E-mail: aisenber@iibce.edu.uy

Abstract. When males have high reproductive investment and female quality is variable, male assessment of sexual partners is expected. *Allocosa alticeps* (Mello-Leitão 1944) is a nocturnal wolf spider that shows a reversal in the sex roles and sexual size dimorphism usual in spiders. Females are the smaller, mobile sex, and they initiate courtship. Males construct burrows that serve as mating refuges and nests for female oviposition and cocoon care. In sex role reversed systems, male mate assessment is expected. Our objective was to test the occurrence of sequential male mate assessment based on female reproductive status and/or body characteristics in *A. alticeps*, discussing the results under sex role reversal hypotheses. We exposed males consecutively to virgin females and mated females and then recorded both courtship performance and mating occurrences relative to individuals' body characteristics. Virgin and mated females detected and entered male burrows in all the cases, and they were courted by males. However, copulations were more frequent with virgin females. The results suggest male mate selectivity in *A. alticeps* is based on female reproductive status. We discuss possible mechanisms underlying male mate choice in this species.

Keywords: Sexual selection, wolf spider, sand dunes, male mate assessment

Traditionally, mate choice studies have focused on female interests, and females are expected to be the exclusively selective sex due to their higher reproductive investment compared to males (Darwin 1871; Andersson 1994). Recent theoretical and empirical evidence shows that when males have high reproductive costs associated with sperm production, mate searching, courtship, copulation, or paternal effort, this sex can also be choosy (Gwynne 1991; Bonduriansky 2001; Clutton-Brock 2007). In sex role reversed systems where male reproductive investment is high and female quality is variable, male mate assessment is expected (Gwynne 1991, 2008; Bonduriansky 2001). Such appears to be the case in the spider *Allocosa alticeps* (Mello-Leitão 1944), a lycosid that shows a reversal in typical sex roles and sexual size dimorphism expected in spiders (Aisenberg & Costa 2008).

Virgin females are expected to provide a higher paternal reproductive success if males are able to monopolize them or minimize female future mating attempts (Carrière & McNeil 1990; Simmons 2001). The preference for virgins over mated females has been reported for several arthropod groups including diverse insects, crayfish, and spiders (Gwynne 1991; Stoltz et al. 2007; Aquiloni & Gherardi 2008). Female fecundity in many arthropods is positively correlated with such traits as body size, weight and body condition (Gwynne 1981; Elwood et al. 1987; Wise & Wagner 1992; Marshall & Gittleman 1994; Uhl et al. 2005), so these variables could also be the target of male mate choice. Most studies report male preference based only on female pheromones (Gasket 2007), but in some cases mate assessment studies include the direct exposure of sexual partners, recording both sexes' responses to all signals exchanged during courtship (Moya-Laraño et al. 2003; Gaskett et al. 2004; Kasumovic et al. 2007; Pruitt & Riechert 2009; Schulte et al. 2010).

Allocosa alticeps is a sex role-reversed nocturnal wolf spider that constructs burrows along the sandy coasts of Uruguay (Aisenberg & Costa 2008). Males are larger than females, and females are the mobile sex that roves searching for males and initiates courtship. Males can respond to female courtship and mount them. Copulation always takes place inside the male burrows. Females prefer to copulate with males that inhabit long burrows (Aisenberg & Costa 2008). After copulation ends, the males exit their burrows, seal the entrances with silk and sand, and leave. Females stay inside male burrows where they will oviposit and exit when it is time for spiderling dispersal (Aisenberg & Costa 2008). Females can lay up to four egg-sacs during the reproductive period, and the first one is the largest in number of eggs (Postiglioni et al. 2008). After clutch emergence, the females will exit male burrows for dispersal of the spiderlings that climb on the female dorsa (Costa et al. 2006). As they are not good diggers (Aisenberg et al. 2010), females will need to copulate again to obtain new male burrows for each oviposition event. As copulations take place exclusively inside their burrows (Aisenberg & Costa 2008), males will need a new deep burrow to have new mating opportunities, and they will be exposed to predation until they construct their new refuge before daylight.

According to sex role reversal hypotheses (Gwynne 1991), males of *A. alticeps* could be selective when making mating decisions. Our objective was to test sequential male mate assessment based on female reproductive status and/or body characteristics in *Allocosa alticeps*. In order to test the central prediction of role reversal, male choosiness among females, we tested male response to consecutive presentations of virgin and mated females of differing body conditions (mass and size). We predicted that males would prefer to copulate with virgins compared to mated females, and with those females that showed high weight values, as a way to maximize their reproductive success. We discuss the results under sex role reversal hypotheses.

METHODS

Natural history.—Individuals reported in earlier studies as *Allocosa* sp. (Capocasale 1990; Costa 1995; Costa et al. 2006; Aisenberg & Costa 2008) were later identified as *Allocosa alticeps* (Aisenberg et al. 2009). Carapace width

averages 2.94 ± 0.30 mm in females and 3.28 ± 0.54 mm in males (Aisenberg et al. 2009). Individuals of *A. alticeps* stay in their burrows during the day and become active during summer nights (Costa 1995). While females construct silk capsules where they remain during daytime, males construct deep and vertical tubular burrows with a single entrance (Capocasale 1990; Aisenberg & Costa 2008). Male burrows average 8.4 ± 1.6 cm length, and 0.8 ± 0.1 cm width (Aisenberg & Costa 2008). Males have specialized setae on the distal section of the pedipalp that aid digging in this sex (Aisenberg et al. 2010). Due to the location of mating, a burrow with a single entrance, and the typical burrow dimensions, we would expect sequential but not simultaneous encounters between a male and more than one female.

Capture and housing.—We collected 22 adult males, 15 mated females (10 with egg-sacs, 5 carrying spiderlings) and 25 sub-adult females of *A. alticeps* in the coastal sand beaches of Marindia, Canelones, Uruguay (34°46′49.9″S, 55°49′34.1″W), from November 2007 to March 2008, and from November 2008 to March 2009. We captured the spiders during the night by using headlamps to locate them walking or leaning out from the burrows, or during daylight by sifting the sand. We housed each spider individually in culture dishes (9.5 cm diam., 1.5 cm height), with sand as substrate and cotton wool soaked in water. We fed individuals three times a week with juvenile cockroaches *Blaptica dubia* (Blattaria: Blaberidae) and mealworm larvae *Tenebrio* sp. (Coleoptera: Tenebrionidae). To obtain virgin females, we daily monitored sub-adults and recorded molting occurrence.

Experimental design.—We performed the trials between December 4 (2007) and April 18 (2008), and between January 2 and March 3 (2009). We used individuals of at least 10 days of adult age, or seven days after their capture at the field. When females were collected with egg-sacs or spiderlings, we removed them and waited ten days before using the spiders in a trial. We fed the animals for the last time 48 h prior to the trials, which began at dusk, coinciding with the period of activity described for the species (Costa 1995).

We carried out the trials in glass cages (30 cm length, 16 cm width, 20 cm height), with a layer of 15 cm of sand as substrate and water supply. We randomly chose individuals for each trial. We placed each male in the arena 48 h prior to the trial, allowing burrow construction. Individuals usually construct their burrows against the glass walls (Aisenberg & Costa 2008), allowing observation and recording of their behaviors inside the burrows. Temperature during the trials averaged 24.63 ± 1.27° C (range: 21–26). We exposed consecutively and randomly each of 15 males of *A. alticeps* to two females of different reproductive status (virgins and mated females). We exposed seven males first to virgin females and the other eight first to mated females. The male's second exposure to a female took place 48 h after the first one. We only considered trials in which the female detected the male burrow within an hour. If courtship did not take place, the trial ended after a 30 min period. We considered "detection" as the point when the female, after contacting the silk of the burrow entrance, stood still and leaned into the male burrow. We considered "female courtship" the moment when the female entered the male burrow and performed sequences of alternative foreleg waving (shaking bouts) (Aisenberg & Costa 2008). The male sometimes responded by shaking his body and forelegs rhythmically. If courtship occurred but copulation did not take place, the trial ended one hour after placing the female in the arena. If copulation occurred, the trial finished after the male covered the burrow entrance and left. We did not reuse females. We also recorded the occurrence of attacks that resulted in injuries, leg loss, and/or cannibalism.

Since males of *A. alticeps* are difficult to obtain in the field because of their highly sedentary condition (Costa et al. 2006), we worked through two experimental periods. We performed five complete trials, exposing one male to one virgin and one mated female during the first experimental period (2007–2008) and conducted the other ten trials during the second time period (2009). We carried out the trials in darkness and recorded with a Sony DCR-SR85 digital video-camera with night-shot. We analyzed the video recordings with J Watcher software (Blumstein et al. 2000). We measured carapace width, a measurement considered representative of body size in spiders (Eberhard et al. 1998), abdominal width and weight of all individuals immediately before the trials. The index abdominal width/carapace width was considered as representative of body condition, as described by Moya-Laraño et al. (2003) for *Lycosa tarantula.* We deposited voucher specimens in the arachnological collection of Sección Entomología, Facultad de Ciencias, Montevideo, Uruguay.

Statistical analysis.—We analyzed data with Past Paleontological Statistics version 1.18 (Hammer et al. 2003) and WINPEPI version 1.6 (Abramson 2004). We compared frequencies with Fisher's exact probability test or the McNemar test for dependent samples (paired test). We checked for normal distribution (Shapiro-Wilk test) and homogeneity of variances (Levene test) of courtship, copulatory, and body characteristics. As variables did not follow parametric conditions, we used the non-parametric Wilcoxon matched-pairs sign test to compare courtship and copulatory characteristics when males were exposed to virgin and mated females. We also performed statistical comparisons between virgin and mated female body characteristics (carapace width and weight) with the non-parametric Mann-Whitney *U*-test. We performed logistic regressions with mated (yes/no) as the response and female mating status, carapace width and weight as predictors.

RESULTS

In all cases, virgin and mated females detected and entered male burrows. All virgins ($n = 15$), and 14/15 mated females performed courtship behavior (McNemar test: $\chi^2 = 1.37$, $P = 0.87$). Virgin females performed more foreleg waving bouts during courtship than mated females (Table 1). However, we did not find significant differences in foreleg waving bouts per minute between virgin and mated females. All males courted virgin females, and 14/15 males courted mated females (McNemar test: $\chi^2 = 0.25$, $P = 0.62$). We did not find differences in courtship duration, male abdominal vibration bouts, or male abdominal vibration bouts per minute between virgin or mated females, but male leg shaking bouts and male leg shaking bouts per minute were higher when males were exposed to virgins than to mated females (Table 1).

We did not find statistical differences in the number of copulations for virgins (Fisher's test: $P = 0.57$), or mated females (Fisher's test: $P = 0.26$) obtained during the first or

Table 1.—Female and male courtship characteristics (median ± quartile) in trials with virgin females and mated females, and results of the statistical comparisons between these two groups (non-parametric Wilcoxon matched-pairs sign test).

	Virgin females	Mated females	Statistics
Females			
Number of leg shaking bouts	27.00 ± 43.50	10.5 ± 9.00	$n_1 = 15$, $n_2 = 14$, $T = 16.00$, $P = 0.04$
Number of leg shaking bouts/min	12.35 ± 4.19	17.24 ± 16.60	$n_1 = 15$, $n_2 = 14$, $T = 40.00$, $P = 0.70$
Courtship duration (min)	3.07 ± 2.38	0.90 ± 1.35	$n_1 = 15$, $n_2 = 15$, $T = 20.00$, $P = 0.07$
Males			
Number of leg shaking bouts	211.98 ± 249.70	53.27 ± 159.82	$n_1 = 15$, $n_2 = 14$, $T = 9.00$, $P = 0.006$
Number of leg shaking bouts/min	6.09 ± 3.69	1.44 ± 4.55	$n_1 = 15$, $n_2 = 14$, $T = 6.00$, $P = 0.01$
Number of abdominal vibration bouts	109.50 ± 155.28	100.04 ± 96.98	$n_1 = 15$, $n_2 = 14$, $T = 28.00$, $P = 0.12$
Number of abdominal vibration bouts/min	5.87 ± 3.24	4.23 ± 5.23	$n_1 = 15$, $n_2 = 14$, $T = 41.00$, $P = 0.75$
Courtship duration (min)	7.19 ± 7.54	4.27 ± 4.77	$n_1 = 15$, $n_2 = 14$, $T = 34.00$, $P = 0.24$

second experimental period. We obtained ten copulations with virgin females and three copulations with mated females. Of the eight males that were exposed first to virgin females and then to mated females, in seven cases copulation occurred only in the first exposure, and in one case mating also occurred in the second exposure. Of the seven males that were introduced first to mated females, in only one case did the male copulate with the mated female, and no re-mating occurred. In three cases, males that had been exposed to mated females first and copulation had not occurred, copulated with virgin females in their second contact. Three males did not copulate in either their first or second meeting. Copulations with mated females were longer (36.82 ± 6.41 min) than copulations with virgin females (21.82 ± 9.83 min) ($U = 1$, $n_1 = 9$, $n_2 = 3$, $P = 0.03$). One mated female was attacked prior to mounting and was cannibalized by the male inside his burrow. In this case, the female had courted but the male had not responded with courtship behavior.

The multiple logistic regression with mated (yes/no) as response and female mating status, carapace width and weight as predictors ($\chi^2 = 9.90$, $df = 3$, $P = 0.02$) showed that reproductive status ($\chi^2 = 6.25$, $df = 1$, $P = 0.01$), but not carapace width ($\chi^2 = 2.58$, $df = 1$, $P = 0.11$), or weight ($\chi^2 = 1.00$, $df = 1$, $P = 0.32$), predicted whether copulation would occur (Table 2). Virgin females showed higher weight values than mated females (median ± quartile: virgins 0.11 ± 0.02 g; mated females 0.08 ± 0.02 g; $U = 41.5$, $n_1 = n_2 = 15$, $P = 0.006$), but we did not find differences in carapace width between the two groups (median ± quartile: virgins 2.70 ± 0.30 mm; mated females 2.50 ± 0.37 mm; $U = 100.5$, $n_1 = n_2 = 15$, $P = 0.86$). Male body size or weight did not seem to affect the occurrence of copulation with virgin or mated females ($\chi^2 = 0.87$, $df = 2$, $P = 0.65$; Table 2).

DISCUSSION

The higher frequencies of male leg shaking bouts and leg shaking bouts per minute performed during courtship and the higher number of matings with virgins compared to mated females correlate with the prediction based on sex role reversal hypotheses (Gwynne 1991; Bonduriansky 2001; Clutton-Brock 2007) that males of *A. alticeps* would be choosy when they make mating decisions. Though both virgin and mated females entered male burrows and performed courtship behavior, males were more prone to mount virgin females. According to the results of the present study, males discriminate between virgin and mated females before mounting. This result was not affected by the order in which the males encountered females of different reproductive status.

Male mate preference biased towards virgin females has been reported for several wolf spiders (Rypstra et al. 2003; Roberts & Uetz 2005; Baruffaldi & Costa 2009) and other spider taxa (Herberstein et al. 2002; Andrade & Kasumovic 2005; Schulte et al. 2010). As we stated earlier, virgin females are associated with greater chances of male paternity success in systems with first male sperm priority (Huber 2005). In *A. alticeps*, females stay inside the male burrow after copulation, oviposit there, and remain buried until they exit the burrow with the spiderlings on their dorsa (Costa et al. 2006). Females can lay up to four consecutive egg-sacs, but the first one is the largest (Postiglioni et al. 2008). Consequently, when males of

Table 2.—Female and male body measurements (median ± quartile) distinguishing when mating occurred or did not occur. Sample sizes (n) are shown between parentheses. Weight measurements of two males that copulated with mated females were lost as a result of human error.

	Virgin females		Mated females	
	Mated ($n = 10$)	Did not mate ($n = 5$)	Mated ($n = 3$)	Did not mate ($n = 12$)
Females				
Carapace width (mm)	2.65 ± 0.37	2.80 ± 0.30	2.50 ± 0.10	2.70 ± 0.55
Body condition index	1.55 ± 0.30	1.44 ± 0.20	1.48 ± 0.12	1.07 ± 0.28
Weight (g)	0.10 ± 0.03	0.11 ± 0.02	0.09 ± 0.01	0.08 ± 0.03
Males				
Carapace width (mm)	3.05 ± 0.35	2.70 ± 0.10	2.70 ± 0.10	3.05 ± 0.50
Body condition index	1.00 ± 0.08	1.00 ± 0.22	1.11 ± 0.11	0.98 ± 0.15
Weight (g)	0.11 ± 0.03	0.09 ± 0.03	0.08	0.10 ± 0.05

A. alticeps copulate with virgin females, they will ensure exclusive paternity of the first and largest clutch.

We did not find differences between mated and virgin females in their approach to male burrows or in the occurrence of courtship. Mated females performed fewer leg shaking bouts during courtship compared to virgins, though we did not find differences in leg shaking bouts per minute or female courtship duration. We do not know the basis of male discrimination, but the lower number of female leg shaking bouts in mated females could reflect a higher sexual reluctance that could also affect male sexual responses. Males might detect subtle differences in courtship behavior, or volatile and/or contact pheromones emitted by females of different mating status, or by previous sexual partners. Nevertheless, mated females entered males' burrows and performed courtship behavior, which suggests that females of this reproductive status are sexually receptive.

Interestingly, when copulations with mated females occurred, they were longer than those of virgin females, as occurs in many arthropods (Simmons 2001). This could suggest the occurrence of sperm displacement mechanisms, plug removal, or intensive stimulation to promote female choice, among other mechanisms described for spiders (Elgar 1995; Eberhard 1996; Huber 2005). The results of the logistic regression suggest that female mating status, but not female body characteristics, is the most important criterion on which males base their mating decisions. When we compared weight between virgin and mated females, virgins were heavier. In this case, it does not mean that female reproductive status and female weight are correlated with male mating acceptance. The logistic regression shows that although virgins are heavier than mated females and males prefer virgins, within each category (virgins or mated) males do not prefer those females showing higher weight values. Characteristics that were not controlled, such as male and female age and male reproductive status, could also affect mate choice in *A. alticeps*, as has been described for other spiders (Gaskett et al. 2004; Uetz & Norton 2007).

In *A. alticeps,* sexual cannibalism has never been reported in the field (Aisenberg et al. 2009) and occurred in only one case in the present study in the absence of male courtship and prior to mounting. This spider is sympatric and synchronic with *Allocosa brasiliensis* (Petrunkevitch 1910), another spider that shows sex role and sexual size dimorphism reversal (Aisenberg et al. 2007). However, males of *A. brasiliensis* frequently show sexual cannibalism on females, reported both in field and laboratory conditions (Aisenberg et al. 2009; Aisenberg et al. 2011). In *A. brasiliensis,* attacks frequently occur after courtship by both sexes and during mounting (Aisenberg et al. 2011). Differences regarding the larger body size, greater longevity (Aisenberg & Costa 2008), and possibly higher energetic requirements in *A. brasiliensis* compared to *A. alticeps* could be affecting mating opportunities and modeling the foraging and sexual strategies of each species.

Future studies will test differences in male mate selectivity when males are exposed to mated females captured with egg sacs or with spiderlings on the dorsa and the effects of male age and reproductive history on mate assessment. We will also test under laboratory conditions if hunger levels and potential mating opportunities affect male mate choice and the occurrence of sexual cannibalism in both *Allocosa* species. Finally, studies about female choice in *A. alticeps* will also help us get a complete picture of the behavioral strategies of the species, elucidating the pressures driving the mating system in this sex role reversed wolf spider.

ACKNOWLEDGMENTS

We are grateful to Luciana Baruffaldi, Fernando G. Costa, Soledad Ghione, Álvaro Laborda, Carlos Perafán, Alicia Postiglioni, Rodrigo Postiglioni, and Carlos Toscano-Gadea for their help during field work. We also thank Fernando G. Costa for his suggestions on the final version of the manuscript. Editor Linden Higgins, Matthias Foellmer, and one anonymous reviewer made useful suggestions that improved the final version of the manuscript. Paul Henderson revised the English. A.A. acknowledges institutional support by PEDECIBA, UdelaR, Uruguay, and financial support by PDT Project 15/63, and the Animal Behavior Society through the Developing Nations Grant.

LITERATURE CITED

Abramson, J.H. 2004. WINPEPI (PEPI-for-Windows): computer programs for epidemiologists. Epidemiologic Perspectives & Innovations 1:6.

Aisenberg, A. & F.G. Costa. 2008. Reproductive isolation and sex role reversal in two sympatric sand-dwelling wolf spiders of the genus *Allocosa*. Canadian Journal of Zoology 86:648–658.

Aisenberg, A., F.G. Costa & M. González. 2011. Male sexual cannibalism in a sand-dwelling wolf spider with sex role reversal. Biological Journal of the Linnean Society 103:68–75.

Aisenberg, A., F.G. Costa, M. González, R. Postiglioni & F. Pérez-Miles. 2010. Sexual dimorphism in chelicerae, forelegs and palpal traits in two burrowing wolf spiders (Araneae: Lycosidae) with sex-role reversal. Journal of Natural History 44:1189–1202.

Aisenberg, A., M. González, Á. Laborda, R. Postiglioni & M. Simó. 2009. Reversed cannibalism, foraging, and surface activities of *Allocosa alticeps* and *Allocosa brasiliensis*: two wolf spiders from coastal sand dunes. Journal of Arachnology 37:135–138.

Aisenberg, A., C. Viera & F.G. Costa. 2007. Daring females, devoted males and reversed sexual size dimorphism in the sand-dwelling spider *Allocosa brasiliensis* (Araneae, Lycosidae). Behavioral Ecology and Sociobiology 62:29–35.

Andersson, M. 1994. Sexual Selection. Princeton University Press, Princeton, New Jersey.

Andrade, M.C.B. & M.M. Kasumovic. 2005. Terminal investment strategies and male mate choice: extreme tests of Bateman. Integrative and Comparative Biology 45:838–847.

Aquiloni, L. & F. Gherardi. 2008. Mutual mate choice in crayfish: large body size is selected by both sexes, virginity by males only. Journal of Zoology 274:171–179.

Baruffaldi, L. & F.G. Costa. 2009. Changes in male sexual responses from silk cues of females at different reproductive states in the wolf spider Schizocosa malitiosa. Journal of Ethology 28:75–85.

Blumstein, D.T., C.S. Evans & J.C. Daniel. 2000. JWatcher 0.9. Online at http://galliform.psy.mq.edu.au/jwatcher/.

Bonduriansky, R. 2001. The evolution of male mate choice in insects: a synthesis of ideas and evidence. Biological Reviews 76:305–339.

Capocasale, R.M. 1990. Las especies de la subfamilia Hippasinae de América del Sur (Araneae, Lycosidae). Journal of Arachnology 18:131–134.

Carrière, Y. & J.N. McNeil. 1990. Effect of age and mating status on the mating behaviour and pheromone titre in alfalfa blotch leafminer females *Agromyza frontella* (Diptera: Agromyzidae). Journal of Insect Physiology 36:457–461.

Clutton-Brock, T. 2007. Sexual selection in males and females. Science 318:1882–1885.

Costa, F.G. 1995. Ecología y actividad diaria de las arañas de la arena *Allocosa* spp. (Araneae, Lycosidae) en Marindia, localidad costera del sur del Uruguay. Revista Brasilera de Biología 55:457–466.

Costa, F.G., M. Simó & A. Aisenberg. 2006. Composición y ecología de la fauna epígea de Marindia (Canelones, Uruguay) con especial énfasis en las arañas: un estudio de dos años con trampas de intercepción. Pp. 427–436. *In* Bases para la conservación y el manejo de la costa uruguaya. (R. Menafra, L. Rodríguez-Gallego, F. Scarabino & D. Conde, eds.). Vida Silvestre, Montevideo.

Darwin, C. 1871. The Descent of Man, and Selection in Relation to Sex. Second edition. John Murray Press, London.

Eberhard, W.G. 1996. Female Control: Sexual Selection by Cryptic Female Choice. Princeton University Press, Princeton, New Jersey.

Eberhard, W.G., B.A. Huber, S.R.L. Rodríguez, R.D. Briceño, I. Salas & V. Rodriguez. 1998. One size fits all? Relationships between the size and degree of variation in genitalia and other body parts in twenty species of insects and spiders. Evolution 52:415–431.

Elgar, M.A. 1995. The duration of copulation in spiders: comparative patterns. Records of the Western Australian Museum Supplement 52:1–11.

Elwood, R.W., J. Gibson & S. Neil. 1987. The amorous *Gammarus*: size assortative mating in *G. pulex*. Animal Behaviour 35:1–6.

Gaskett, A.C. 2007. Spider sex pheromones: emission, reception, structures, and functions. Biological Reviews 82:27–48.

Gaskett, A.C., M.E. Herberstein, B.J. Downes & M.A. Elgar. 2004. Changes in male mate choice in a sexually cannibalistic orb-web spider (Araneae: Araneidae). Behaviour 141:1197–1210.

Gwynne, D.T. 1981. Sexual difference theory: mormon crickets show role reversal in mate choice. Science 213:779–780.

Gwynne, D.T. 1991. Sexual competition among females: what causes courtship-role reversal? Trends in Ecology & Evolution 6:118–121.

Gwynne, D.T. 2008. Sexual conflict over nuptial gifts in insects. Annual Review of Entomology 53:83–101.

Hammer, O., D.A.T. Harper & P.D. Ryan. 2003. PAST- PAlaeontological STatistics, Version 1.18. Copyright Hammer & Harper. Online at http://folk.uio.no/ohammer/past.

Herberstein, M.E., J.M. Schneider & M.A. Elgar. 2002. Costs of courtship and mating in a sexually cannibalistic orb-web spider: female mating strategies and their consequences for males. Behavioral Ecology and Sociobiology 51:440–446.

Huber, B. 2005. Sexual selection research on spiders: progress and biases. Biological Reviews 80:363–385.

Kasumovic, M.M., M.J. Bruce, M.E. Herberstein & M.C.B. Andrade. 2007. Risky mate search and mate preference in the golden orb-web spider (*Nephila plumipes*). Behavioral Ecology 18:189–195.

Marshall, S.D. & J.L. Gittleman. 1994. Clutch size in spiders: is more better? Functional Ecology 8:118–124.

Moya-Laraño, J., J. Pascual & D.H. Wise. 2003. Mating patterns in late-maturing female Mediterranean tarantulas may reflect the costs and benefits of sexual cannibalism. Animal Behaviour 66:469–476.

Postiglioni, R., M. González & A. Aisenberg. 2008. Permanencia en la cueva masculina y producción de ootecas en dos arañas lobo de los arenales costeros. Proceedings IX Jornadas de Zoología del Uruguay:145.

Pruitt, J.N. & S.E. Riechert. 2009. Male mating preference is associated with risk of pre-copulatory cannibalism in a socially polymorphic spider. Behavioral Ecology and Sociobiology 63:1573–1580.

Roberts, J.A. & G.W. Uetz. 2005. Information content of chemical signals in the wolf spider, *Schizocosa ocreata*: male discrimination of reproductive state and receptivity. Animal Behaviour 70: 217–223.

Rypstra, A.L., C. Wieg, S.E. Walker & M.H. Persons. 2003. Mutual mate assessment in wolf spiders: differences in the cues used by males and females. Ethology 109:315–325.

Schulte, K.F., G. Uhl & J.M. Schneider. 2010. Mate choice in males with one-shot genitalia: limited importance of female fecundity. Animal Behaviour 80:699–706.

Simmons, L.W. 2001. Sperm Competition and its Evolutionary Consequences in the Insects. Princeton University Press, Princeton, New Jersey.

Stoltz, J.A., J.N. McNeil & M.C.B. Andrade. 2007. Males assess chemical signals to discriminate just-mated females from virgins in redback spiders. Animal Behaviour 74:1669–1674.

Uetz, G.W. & S. Norton. 2007. Preference for male traits in female wolf spiders varies with the choice of available males, female age and reproductive state. Behavioral Ecology and Sociobiology 61:631–641.

Uhl, G., S. Schmitt & M. Shäfer. 2005. Fitness benefits of multiple mating versus female mate choice in the cellar spider (*Pholcus phalangioides*). Behavioral Ecology and Sociobiology 59:69–76.

Wise, D.H. & J.D. Wagner. 1992. Evidence of exploitative competition among young stages of the wolf spider *Schizocosa ocreata*. Oecologia 91:7–13.

Manuscript received 2 March 2011, revised 8 September 2011.

2011. The Journal of Arachnology 39:449–453

Chemical prey cues influence the urban microhabitat preferences of Western black widow spiders, *Latrodectus hesperus*

Amanda Johnson, **Orenda Revis** and **J. Chadwick Johnson**[1]: Arizona State University at the West Campus, Division of Mathematical and Natural Sciences (2352), 4701 West Thunderbird Road, Glendale, Arizona 85306 USA

Abstract. Spiders are important predators in terrestrial ecosystems, and several spider species have been shown to use chemical cues to locate prey. However, the extent to which chemical prey cues actually drive habitat use by individual spiders remains unclear. In this study we tested whether Western black widow spiders, *Latrodectus hesperus* Chamberlin & Ivie 1935, can detect chemical cues left by potential prey items and adjust their habitat preferences (i.e., web building behavior and refuge choice) accordingly. Using outdoor enclosures, we gave mature female widows the choice of microhabitat (rocks) previously housing cricket prey versus control rocks lacking cricket cues. Our results showed a significant preference by black widows to build their webs in areas that contain chemical prey cues. We discuss the implications of this finding for our understanding of urban black widow habitat use, population dynamics, and the potential for urban infestations.

Keywords: Foraging kairomone, urban ecology, web building, predation

Despite being the oldest method of animal communication, olfaction and chemical communication have historically been less studied than visual and acoustic communication (Bradbury & Vehrencamp 1998). However, development of insect model systems has allowed for great advances in the field of chemical ecology (reviewed in Symonds & Elgar 2008). For example, insect models have helped identify the widespread prevalence of sexual pheromones that bring males and females together, sometimes from great distances, and initiate the mating sequence (Cardé & Minks 1995). In addition, predator-prey studies involving arthropods have been instrumental in the rapidly growing study of kairomones, chemical cues emitted by a sender that are exploited by a receiver (Dicke & Sabelis 1988; Dicke & Grostal 2001; see Ruther et al. 2007 for expanded definitions of kairomones). In particular, foraging kairomones allow predators to locate prey (e.g. Clark et al. 2000; Punzo 2006), and enemy-avoidance kairomones allow prey to avoid predators (Kortet & Hedrick 2004). Thus, chemical signals are a critical factor shaping the evolution of arthropod mating systems and predator-prey dynamics.

Despite a historical emphasis on web-based, vibratory communication, spiders have proven effective model species for the study of pheromonal communication (reviewed in Gaskett 2007; Schulz et al. 2004). In contrast, the study of chemical cues mediating predator-prey dynamics involving spiders has received less attention, despite the widespread belief that spiders are key predators of terrestrial ecosystems (Wise 1993). One system that has received considerable attention in this respect involves the wolf spider *Hogna helluo* (Walckenaer 1837) and its syntopic prey species, the smaller wolf spider, *Pardosa milvina* (Hentz 1844). Wolf spiders (Lycosidae) are a wandering, non web-building taxon found in great abundances in agricultural ecosystems of the United States (Marshall & Rypstra 1999). From the perspective of predation risk, *P. milvina* exhibit anti-predator behavioral responses to airborne (Schonewolf et al. 2006) as well as silk and excreta-based, chemical cues from *H. helluo* (Persons et al. 2001, 2002; Lehmann et al. 2004). Conversely, from the perspective of prey availability, *H. helluo* recently fed *P. milvina* prefer areas laden with chemical cues from *P. milvina*, whereas *H. helluo* recently fed crickets prefer areas laden with chemical cues from crickets (Persons & Rypstra 2000). A similar preference for patches laden with cricket chemical cues has been shown for the wolf spider, *Schizocosa ocreata* (Persons & Uetz 1996). Thus, chemical cues from prey play an important role in shaping the foraging behavior of wolf spiders.

Given that spiders are predators thought to limit insect populations, it is surprising that more studies have not tested the ability of non-lycosid spiders to detect chemical cues from their prey (but see Suter et al.1989; Allan et al. 1996; Clark et al. 2000 for a few examples). Particularly lacking are field/mesocosm studies of kairomone use by web-building spiders that examine spider habitat/web building preferences outside of the laboratory. Web-building spiders make a critical microhabitat selection decision when they invest the time and energy required to build and maintain a web. Optimal web location is likely influenced by food availability, predation risk, and competition (Smallwood 1993), as well as other factors (e.g. body condition, see reviews by Janetos 1986; Rieehert & Gillespie 1986; Herberstein & Tso 2011). Thus, selection might favor web placement in areas of prey abundance, and chemical cues from prey are one cue of prey availability/abundance.

Here we test the idea that a locally abundant web-building spider, the Western black widow (*Latrodectus hesperus* Chamberlin & Ivie 1935), uses chemical prey cues to determine where to place its web. Widow spiders *(Latrodectus* spp.*)* are perhaps best known for the potency of their venom (Orlova et al., 2000) and the medical concern these toxins present to human victims (Muller 1993; Gonzalez 2001). Moreover, widow spiders have proven to be outstanding urban, agricultural and invasive pests (Costello & Daane 1999; Daane et al. 2004; Garb et al. 2004). In particular, *L. hesperus* populations in urban habitats of Phoenix, Arizona (e.g.,

[1] Corresponding author. jchadwick@asu.edu.

schoolyards) can reach 0.28 spiders/m^2, with reduced nearest neighbor distances (mean = 1.9 m) relative to populations from surrounding, undisturbed Sonoran desert habitat (density = 0.006 spiders/m^2 and nearest neighbor distance > 50 m; Johnson unpub. data). *Latrodectus hesperus* males use silken cues from females in a courtship context (Ross & Smith 1979; Johnson et al. 2011), and widow web architecture is condition dependent, with spiders adaptively allotting more to sticky, prey-capture silk when prey are limiting (Blackledge & Zevenbergen 2007). Here we present the first study to ask whether or not this common urban pest bases its microhabitat preferences on chemical cues from prey. Specifically, we utilize an outdoor enclosure that mimics urban habitat and test the prediction that female *L. hesperus* will preferentially choose habitat patches that have recently housed cricket prey for their webs.

METHODS

Housing.—We used an outdoor facility on the grounds of Arizona State University's West campus approximately 7 m^2 in area and 165 cm tall, contained on the sides by chain link fencing and with a chicken wire ceiling. Within this facility, a metal wall (0.75 m tall) was buried into the ground to create a 6-m^2 enclosure. Within this enclosure, we buried aluminum flashing into the soil to divide the enclosure into 16 cells of equal area (25 cm tall, 1.5 m^2) to maintain individual spiders/webs.

Within each of the 16 cells, one commercially-purchased river rock (average diam. = 25.5 cm) was placed in each of the four corners. To minimize pre-experiment chemical cues that rocks may have been exposed to before purchase, we submerged all rocks in water for 48 h, scrubbed rock surfaces with a metal pad and rinsed rocks with water before use. Thus, non-experimental cues were minimized, and all rocks used were treated in the above manner before being used. Rocks were used in only one trial.

Establishing prey chemical cues.—One rock/corner from each of the 16 cells was randomly selected to be charged with cricket chemical cues (hereafter referred to as 'prey-cue corners'). In order to "charge" the rock with the prey chemical cues, we housed five adult house crickets (*Acheta domesticus*) for five continuous days under a plastic, translucent tub (48 cm × 308 cm × 14 cm LWH), upturned to contain the experimental rock. Prey-cue corners were inspected daily, and dead crickets were removed and replaced. After five days, plastic tubs and crickets were removed. Finally, prey-cue corners were finished by the addition of egg crate (10 ×10 × 4 cm LWH) that crickets had been shipped in to provide additional chemical cues. This same size of egg crate, purchased from a local grocery store (i.e., housing chicken eggs but not arthropods), was added to each of the non prey-cue corners.

Experimental procedure.—We collected 48 penultimate-stage juvenile females from urban Phoenix habitats in April 2009. Spiders were housed individually in the laboratory in plastic, transparent containers (10 × 10 × 13 cm LWH) and fed one adult house cricket weekly until trials began. Spiders matured in the laboratory within two to three weeks of collection and were used in trials within the first four weeks of maturity. Spiders were weighed (mg) and had their cephalothorax digitally imaged immediately prior to use. We estimated fixed adult body size from this single image as the length (mm) of the tibia from a fourth leg using Zoombrowser™. We calculated spider body condition as both the residuals of a linear regression of body mass on tibia length (Jakob et al. 1996), as well as body mass corrected for tibia length (Moya-Larano et al. 2008). As these condition measures yielded similar results, we used mass corrected for tibia length in the analyses reported.

Trials were conducted in May 2009, when average daily temperatures in Phoenix ranged from lows of ~ 12° C to highs of ~ 30° C. At 1900 hours, spiders were randomly chosen and released in the center of each cell. We recorded initial direction of movement and then scored the location of each spider every 15 min for 90 min. Any spiders not located during a check were assumed to be hiding within the cell (under rocks or egg crate) and allowed to remain hiding for three consecutive intervals. On the fourth "hiding" interval, egg crates and rocks were gently maneuvered to determine the location of the spider. Spiders were assumed to have been in this location for the entirety of the "hiding" interval. In the cases in which a spider was found moving within its cell, we scored the spider's location as the corner toward which the spider moved. The following day we scored each spider's location again at 0900 and 1800 h. On the third day after introduction, we made a final 0900 h observation, and considered this to be each spider's final habitat selection. We used this third morning location as our measure of habitat selection, because no spider relocations occurred for five days after this date, and all spiders not missing (n = 32 spiders out of 48 released, see below) had begun to build extensive webs out from the rock they were using as a daytime refuge.

Statistical analysis.—We conducted three block replicates of this experiment - each using an independent sample of spiders and rocks. The aluminum sides and dirt floor of each cell was sprayed with water through a high pressure hose and allowed to air-dry over the course of at least seven days before the next block replicate began. The location of the prey-cue corner in a cell was randomly selected before each trial. Thus, although we cannot claim to have removed all residual chemical cues from crickets and previous spiders, our aim was to minimize these previous cues so as not to interfere with our manipulation of prey-cue corners. We view the evidence below that habitat preferences did not differ between our three block replicates as evidence that we succeeded in minimizing the accumulation of cues across blocks.

In block 1, 12/16 spiders were accounted for after three days. In block 2, 13/16 spiders were accounted for after three days. In block 3, 7/16 spiders were accounted for after three days. Thus, across three blocks of the experiment 32 spiders established webs (see below for a discussion of the fate of the 16 missing spiders). Missing spiders were excluded from habitat preference analyses. All analyses were conducted using SPSS. For each block replicate the observed frequency of habitat choice of prey-cue corners by spiders (at Day 3) was compared to that expected by random chance (25%) and analyzed with G-tests. In addition, binary logistic regression was used to test the hypothesis that female condition explained habitat choice (choice of prey cue corner or choice of non prey-cue corner), and multinomial logistic regression was used to examine habitat choosiness (i.e., the number of habitat switches exhibited across the course of the three-day trial; range 0–3).

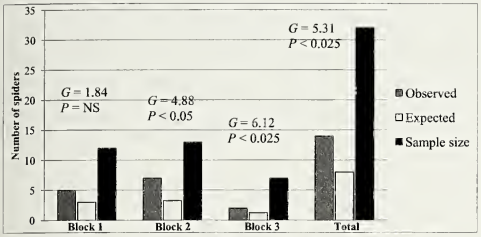


Figure 1.—The number of spiders observed to select prey-cue corners was consistently greater than that expected based on chance. Three consecutive blocks of the experiment are presented, followed by a summation of all three blocks.

RESULTS

Sixty-seven percent (32/48) of the females settled successfully within their cell after three days (i.e., did not escape or get preyed upon: see Discussion). As the habitat choice preferences of missing spiders cannot be known, below we exclude the 16 data points for missing females. All the females not missing settled under one of the four rocks provided as refuge and built their webs out from this substrate. Because rocks were the only refuge from which webs were built, and given that each cell was provisioned with four, evenly spaced rocks, female habitat choice consisted of one of these four options. Black widow females were significantly more likely to select prey-cue corners/rocks for their webs (14/32 = 44%) than would be expected by chance (25% * 32 = 8; $G = 5.29$, $P < 0.05$). As seen in Fig. 1, spider preference for prey-cue corners fluctuated in intensity across the three waves of the experiment, though females were always observed to choose prey-cue corners more often than expected by chance. In addition, using a single heterogeneity G-test (Sokal & Rohlf 1995:715), we found no significant differences in habitat choice across these three repeated blocks of the experiment ($G = 1.24$, $0.25 < P < 0.5$) and thus feel justified in pooling data across blocks.

Female body condition did not predict habitat choice. Binary logistic regression indicated that female body condition (mass corrected for leg length) was a poor predictor of both 1) the original 'choice' to settle under a rock ($n = 48$, $\chi^2 = 0.765$, $P = 0.382$), and 2) the subsequent 'choice' by spiders that settled on a rock to settle on rocks charged with prey cues (266.90 ± 28.5 mg) or not (279.1 ± 20.5 mg; $n = 32$, $\chi^2 = 1.50$, $P = 0.220$). In addition, linear regression indicated that body condition was a poor predictor of the number of habitat switches ("choosiness)", range 0–3) exhibited over the three-day trial ($R^2 = 0.06$, $F_{1,30} = 0.86$, $P = 0.37$), and multinomial logistic regression suggests that this number of switches was a poor predictor of whether the spider eventually chose a prey-cue corner or non-prey-cue corner or was missing ($n = 48$, $\chi^2 = 5.68$, $P = 0.46$). Thus, habitat choice seems to be more strongly shaped by prey cues than by body condition, and we found no suggestion that a spider's ultimate (Day 3) habitat choice was affected by the number of times a spider changed its habitat (choosiness).

DISCUSSION

Our results indicate that urban black widow females preferentially settle in microhabitats/refuges that have been charged with chemical cues from cricket prey. Thus, although *Latrodectus* spp. are known to use chemical cues from conspecific silk in courtship and cannibalism contexts (Stoltz et al. 2007; Johnson et al. 2011), *L. hesperus* females are also capable of detecting chemical cues from potential heterospecific prey items. However, we found no evidence that female body condition affected habitat choice for prey availability. It should be noted, however, that we did not manipulate body condition, and thus it remains to be seen whether extreme variation in body condition might intensify habitat-choice decisions for prey cues. Nevertheless, the present evidence that black widows settle near cricket chemical cues adds to the list of spiders known to use foraging kairomones and has important implications for the control of urban infestations.

Our finding that widow spiders use chemical prey cues in their habitat choice has potential implications for the management of urban black widow infestations. The medical importance of this species combined with its ability to form dense urban infestations has led to heightened pesticide usage, and therefore we suggest it is critical that we understand what cues from urban habitat are being used by widow spiders to determine their habitat preferences. If urban widow infestations track the abundance of urban arthropod prey, then the pesticide applications that often follow widow infestations may be effective in controlling widow abundance indirectly by controlling their prey. Although pesticides broadly applied are generally ineffective at directly killing black widows (J.C. Johnson pers. obs.), prey elimination may limit urban widow infestations.

However, such strategies may have unintended negative consequences. Specifically, very little is known about the ability of arthropod pests to behaviorally avoid pesticides. If pesticides are broadly applied, for example, along the perimeter of a schoolyard, the result could be the dispersal of crickets into surrounding areas rather than cricket mortality. Indeed, few data are available to assess the degree to which widespread pesticide applications actually kill urban arthropods, and studies on non-target species indicate that insecticide irritability (avoidance after contact) and insecticide repellence (avoidance without contact) occur frequently (Cordeiro et al. 2010). Anecdotally, our laboratory (one of the few to ban University-sponsored pesticide applications) experiences this behavioral avoidance of pesticides and is overrun by roaches soon after surrounding laboratories are treated. If urban prey are driven away from pesticides instead of killed, then cricket abundance may be lessened in pesticide-treated areas, but will be heightened in surrounding areas—thereby encouraging black widow spiders to relocate. The resultant cycle (i.e., widow infestation, pesticide application, prey relocation, widow infestation) seems a dubious pest control strategy given the costs (financial and environmental health) of wide-scale pesticide usage. We are currently investigating the effects of multiple stressors (pesticides and predation risk) on both urban black widows and their prey.

During this study, we "lost" 1/3 of the spiders released. Although two of these spiders were documented as cannibalized in a neighboring cell, we could not account for the remaining 14 spiders. Despite the fact that the walls that surround our enclosure are 0.75 m. tall and made of slick

aluminum, it is possible that spiders climbed these walls and escaped, though we have never witnessed nor found draglines indicating an escape. In our opinion, it is more likely that the majority of these missing spiders were preyed upon within their cells by vertebrate predators, a possibility that is supported by our finding spider legs in vacated cells. Supporting this hypothesis, we regularly found the native tree lizard *Urosaurus ornatus* as well as the exotic Mediterranean gecko *Hemidactylus turcicus* within spider cells despite our attempts to exclude these predators from the area. Although we can find no report of these species feeding upon *L. hesperus*, we have since verified that when confined with black widows, both species do kill and consume large female widow spiders with no apparent negative effects. We suggest that urban lizards/geckos, widow spiders and crickets offer an outstanding tri-trophic interaction upon which to base the development of an urban food web for the Phoenix metropolitan area.

LITERATURE CITED

Allan, R.A., M.A. Elgar & R.J. Capon. 1996. Exploitation of an ant chemical alarm signal by the zodariid spider *Habronestes bradleyi* Walckenaer. Proceedings of the Royal Society of London B 263:69–73.

Blackledge, T.A. & J.M. Zevenbergen. 2007. Condition-dependent spider web architecture in the western black widow, *Latrodectus hesperus*. Animal Behaviour 73:855–864.

Bradbury, J.W. & S.L. Vehrencamp. 1998. Principles of Animal Communication. Sinauer, Sunderland, Massachusetts.

Cardé, R.T. & A.K. Minks. 1995. Control of moth pests by mating disruption-successes and constraints. Annual Review of Entomology 40:559–585.

Clark, R.J., R.R. Jackson & B. Cutler. 2000. Chemical cues from ants influence predatory behavior in *Habrocestum pulex*, an ant-eating jumping spider (Araneae, Salticidae). Journal of Arachnology 28: 309–318.

Cordeiro, E.M.G., A.S. Correa, M. Venzon & R.N.C. Guedes. 2010. Insecticide survival and behavioral avoidance in the lacewings *Chrysoperla externa* and *Ceraeochrysa cubana*. Chemosphere 81: 1352–1357.

Costello, M.J. & K. Daane. 1999. Abundance of spiders and insect predators on grapes in Central California. Journal of Arachnology 27:531–538.

Daane, K.M., P. Hernandez, G.Y. Yokota, W.J. Bentley & A.B. Lawson. 2004. Control tactics and field biology for black widow spiders in table grapes. *In* 2003–2004. Viticulture Research Report (California Table Grape Commission Annual Report), Volume 32.

Dicke, M. & P. Grostal. 2001. Chemical detection of natural enemies by arthropods: an ecological perspective. Annual Review of Ecology and Systematics 32:1–23.

Dicke, M. & M.W. Sabelis. 1988. Infochemical terminology: based on cost-benefit analysis rather than origin of compounds. Functional Ecology 2:131–139.

Garb, J.E., R.G. Gillespie & A. Gonzalez. 2004. The black widow spider genus *Latrodectus* (Araneae, Theridiidae): phylogeny, biogeography, and invasion history. Molecular Phylogenetics and Evolution 31:1127–1142.

Gaskett, A. 2007. Spider sex pheromones: emission, reception, structures, and functions. Biological Reviews of the Cambridge Philosophical Society 82:27–48.

Gonzalez, F. 2001. Black widow bites in children. Journal of the American Osteopathic Association 101:229–231.

Herberstein, M. & I. Tso. 2011. Spider webs: evolution, plasticity and diversity. Pp. 57–98. *In* Spider Behavior: Flexibility and Versatility. (M. Herberstein, ed.). Cambridge University Press, Cambridge, UK.

Jakob, E.M., S.D. Marshall & G.W. Uetz. 1996. Estimating fitness: a comparison of body condition indices. Oikos 77:61–67.

Janetos, A.C. 1986. Web-site selection: are we asking the right questions? Pp. 9–22. *In* Spiders: Webs, Behavior, and Evolution. (W.A. Shear, ed.). Stanford University Press, Stanford, California.

Johnson, J.C., P. Trubl, V. Blackmore & L. Miles. 2011. Male black widows court well-fed females more than starved females: silken cues indicate sexual cannibalism risk. Animal Behaviour 82: 383–390.

Kortet, R. & A. Hedrick. 2004. Detection of the spider predator, *Holoena nedra*, by naïve juvenile field crickets (*Gryllus integer*) using indirect cues. Behaviour 141:1189–1196.

Lehmann, L.M., S.E. Walker & M.H. Persons. 2004. The influence of predator sex on chemically mediated antipredator response in the wolf spider *Pardosa milvina* (Araneae, Lycosidae) Ethology 110: 323–339.

Marshall, S.D. & A.L. Rypstra. 1999. Patterns in the distribution of two wolf spiders (Araneae, Lycosidae) in two soybean agroecosystems. Environmental Entomology 28:1052–1059.

Moya-Larano, J., R. Macias-Ordonez, W.U. Blanckenhorn & C. Fernandez-Montraveta. 2008. Analyzing body condition: mass, volume or density? Journal of Animal Ecology 77:1099–1108.

Muller, G.J. 1993. Black and brown widow spider bites in South Africa—a series of 45 cases. South African Medical Journal 83: 399–405.

Orlova, E.V., M.A. Rahman, B. Gowen, K.E. Volynski, A.C. Ashton, C. Maanser, M. Van Heel & Y.A. Ushkaryov. 2000. Structure of alpha-latrotoxin oligomers reveals that divalent cation-dependent tetramers form membrane pores. Nature Structural & Molecular Biology 7:48–53.

Persons, M.H. & A.L. Rypstra. 2000. Preference for chemical cues associated with recent prey in the wolf spider *Hogna helluo* (Araneae, Lycosidae). Ethology 106:27–35.

Persons, M.H. & G.W. Uetz. 1996. Wolf spiders vary patch residence time in the presence of chemical cues from prey (Araneae, Lycosidae). Journal of Arachnology 24:76–79.

Persons, M.H., S.E. Walker & A.L. Rypstra. 2001. Wolf spider predator avoidance tactics and survival in the presence of diet-associated predator cues (Araneae, Lycosidae). Animal Behaviour 61:43–51.

Persons, M.H., S.E. Walker & A.L. Rypstra. 2002. Fitness costs and benefits of antipredator behavior mediated by chemotactile cues in the wolf spider *Pardosa milvina* (Araneae, Lycosidae). Behavioral Ecology 13:386–392.

Punzo, F. 2006. Female spider wasps, *Anoplius splendens* Driesbach (Hymenoptera, Pompilidae), learn to associate the odor of host feces with the presence of the host. Journal of Entomological Science 41:202–210.

Riechert, S.E. & R.G. Gillespie. 1986. Habitat choice and utilization in web building spiders. Pp. 23–48. *In* Spiders: Webs, Behavior, and Evolution. (W.A. Shear, ed.). Stanford University Press, Stanford, California.

Ross, K. & R.L. Smith. 1979. Aspects of the courtship behavior of the black widow spider, *Latrodectus hesperus* (Araneae, Theridiidae), with evidence for the existence of a contact sex pheromone. Journal of Arachnology 7:69–77.

Ruther, J., L.M. Stahl, S. Steiner, L.A. Garbe & T. Tolasch. 2007. A male sex pheromone in a parasitic wasp and control of the behavioral response by the female's mating status. Journal of Experimental Biology 210:2163–2169.

Schonewolf, K.W., R. Bell & A.L. Rypstra. 2006. Field evidenee of an airborne enemy-avoidance kairomone in wolf spiders. Journal of Chemical Ecology 32:1565–1576.

Schulz, S., J. Fuhlendorff, J.L.M. Steidle, J. Collatz & J.T. Franz. 2004. Identification and biosynthesis of an aggregation pheromone of the storage mite *Chortoglyphus arcuatus*. ChemBioChem 5: 1500–1507.

Smallwood, P.D. 1993. Web-site tenure in the long-jawed spider - Is it risk-sensitive foraging, or conspecific interactions. Ecology 74: 1826–1835.

Sokal, R.R. & F.J. Rohlf. 1995. Biometry. Third edition. W.H. Freeman, New York.

Stoltz, J.A., J.N. McNeil & M.C.B. Andrade. 2007. Males assess chemical signals to discriminate just-mated females from virgins in redback spiders. Animal Behaviour 74:1669–1674.

Suter, R.B., M. Shane & A.J. Hirscheimer. 1989. Spider vs. spider - *Frontinella pyramitela* detects *Argyrodes trigonum* via cuticular chemicals. Journal of Arachnology 17:237–240.

Symonds, M.R.E. & M.A. Elgar. 2008. The evolution of pheromone diversity. Trends in Ecology & Evolution 23:220–228.

Wise, D.H. 1993. Spiders in Ecological Webs. Cambridge University Press, Cambridge, UK.

Manuscript received 22 February 2011, revised 11 September 2011.

2011. The Journal of Arachnology 39:454–481

Taxonomy of the *Leiobunum calcar* species-group (Opiliones: Sclerosomatidae: Leiobuninae)

Elizabeth A. Ingianni[1], **Charles R. McGhee**[2] and **Jeffrey W. Shultz**[1,3]: [1]Department of Entomology, University of Maryland, College Park, Maryland 20742, USA; [2]Department of Biology, Middle Tennessee State University, Murfreesboro, Tennessee 37132, USA

Abstract. The *Leiobunum calcar* species-group is erected to accommodate four species of North American harvestmen, namely, *L. nigropalpi* (Wood 1868), *L. euserratipalpe* new species, *L. calcar* (Wood 1868) and *L. hoffmani* new species. The group is characterized by several sexually dimorphic characters, including an elongate penis lacking subterminal sacs, base of male palpal tibia projecting ventrally and denticulate, and unique female sterno-opercular mechanism that appears to act as a pregenital barricade. The four species are distinguished by penial and palpal features in the male and by details of the sterno-opercular mechanism in females. The history of confusion between *L. serratipalpe* Roewer 1910 and *L. calcar* is reviewed, and the new species *L. euserratipalpe* is proposed to accommodate the concept of *L. serratipalpe* developed by North American systematists as well as the synonymy of *L. serratipalpe* Roewer with *L. calcar*. All species are diagnosed, described and illustrated, and a key to species is provided.

Keywords: Harvestman, systematics, North America

The Opiliones fauna of the eastern and central parts of the United States and Canada is dominated by the "daddy longlegs" of the sclerosomatid subfamily Leiobuninae. With over 20 species, *Leiobunum* is the most species-rich genus in this region and also occurs in the Euro-Mediterranean Region and northeastern Asia as well as an area including Mesoamerica and the western USA and Canada. A recent phylogenetic analysis (Hedin et al. in press) has shown that each of these four regions is home to one or more *Leiobunum* clades that are more closely related to non-*Leiobunum* species in the same region than to the *Leiobunum* species from different regions. This insight demonstrates the need for significant taxonomic reorganization within *Leiobunum* and Sclerosomatidae generally, but it may also accelerate phylogenetic analysis and taxonomic revision within each regional clade. Specifically, intensive systematic analyses of regional taxa can now be undertaken with a low probability that closely related but geographically distant members will be overlooked. Indeed, the leiobunine fauna of North America is in particular need of taxonomic revision, and the current study was undertaken in part to capitalize upon these recent phylogenetic insights.

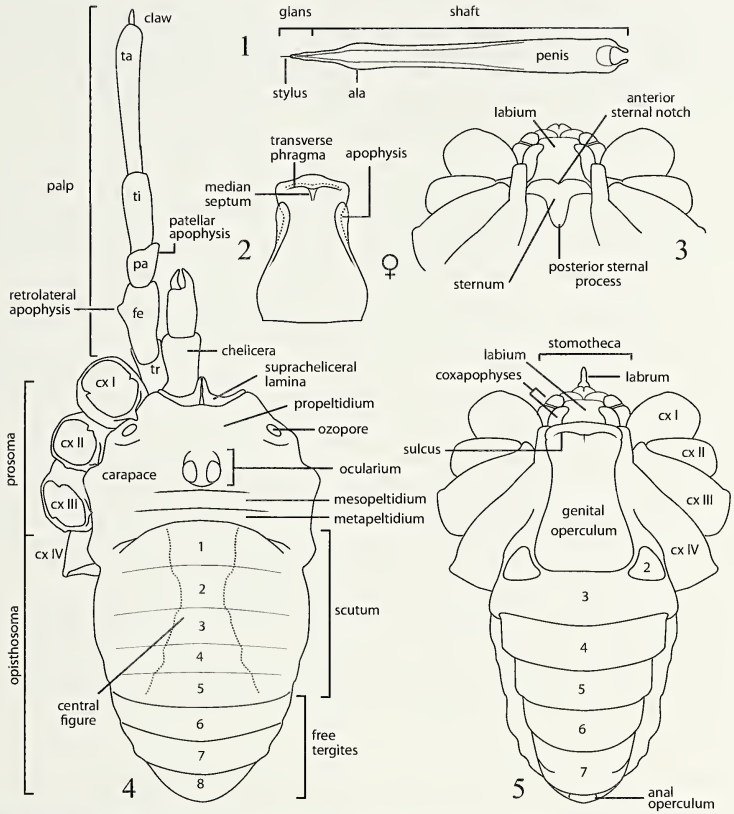
In an unpublished portion of his doctoral dissertation, McGhee (1970) delimited a small group of leiobunine harvestmen from eastern North America, the *Leiobunum calcar* species-group. The group encompassed two widely accepted species, *L. calcar* (Wood 1868) and *L. nigropalpi* (Wood 1868), as well as *L. serratipalpe* Roewer 1910 (subsequently synonymized with *L. calcar* by Cokendolpher 1981) and two undescribed species, *L. cumberlandense* and *L. hoffmani*. The *calcar* group was united by male characters, including a long penis lacking sacs or bulbs, palpal tibiae with an enlarged proximoventral surface with denticles, and, in most species, an apophysis or cluster of denticles on the subterminal retrolateral surface of the palpal femora. Here we assess McGhee's taxonomic proposals concerning the *L. calcar* group using a geographically diverse sample of specimens and a newly discovered suite of female characters, the sterno-opercular mechanism (Figs. 2, 3). The sternum (*arculi genitales*) is a sclerite that spans the ventral body surface between coxae III and is typically hidden by the anterior margin of the genital operculum. The sternum and operculum fit together to form an apparent barricade in females of *Leiobunum* species in which the penis lacks gift-bearing sacs. The taxonomic conclusions of our study concur with those of McGhee (1970) in recognizing the long-established species *L. calcar* and *L. nigropalpi* as well as the new species *L. hoffmani*. However, we consider *L. cumberlandense* to be a regional variant of *L. calcar*. In addition, we propose the name *L. euserratipalpe* for the species that American arachnologists called *L. serratipalpe* Roewer (Davis 1934; Bishop 1949; Edgar 1966; McGhee 1970) before the type specimen was shown to be a female *L. calcar* (Cokendolpher 1981).

[3]Corresponding author. Email: jshultz@umd.edu

METHODS

Morphology.—We examined all specimens in either isopropanol or ethanol, depending on the medium used by their home repositories. Dissections were performed using a needle and microscissors under a Leica MZ APO dissecting microscope with a 1× or 0.63× objective lens. Photos were obtained using PaxCam3 in Adobe Photoshop, and composite photos were created and edited in Helicon Focus software. We prepared illustrations in Adobe Illustrator from the composite photos and made measurements with a stage micrometer, ocular scale and drawing tube.

Specimen repositories.—We obtained specimens used in this study from the following museums and repositories: American Museum of Natural History, New York (AMNH); Academy of Natural Sciences of Philadelphia (ANSP); Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (MCZ); Mississippi Entomology Museum, Mississippi State University (MEM); North Carolina Museum of Natural Sciences, Raleigh (NCMNS); National Museum of Natural History, Smithsonian Institution, Washington, D.C. (NMNH); U.S. National Park Service (NPS); University of Maryland, J.W. Shultz Collection, College Park (UMD); Virginia Museum of Natural History, Martinsville (VMNH).



Figures 1–5.—Basic anatomy of the *Leiobunum calcar* species-group: 1. Penis, dorsal perspective; 2. Ventral view of female with genital operculum removed showing sternum (opisthosomal sternite 1); 3. Female genital operculum, detached, showing dorsal (inner) surface; 4. Dorsal view of male, with opisthosomal tergites numbered; 5. Ventral view of male, with opisthosomal sternites numbered. Abbreviations: cx, coxa; fe, femur; pa, patella; ta, tarsus; ti, tibia; tr, trochanter.

TAXONOMY

Family Sclerosomatidae Simon 1879
Subfamily Leiobuninae Banks 1893
Genus *Leiobunum* C.L. Koch 1839

Type species.—*Phalangium rotundum* Latreille 1798, by subsequent designation (Simon 1879:172)

Leiobunum calcar new species-group

Diagnosis.—Penis long (> 2/3 length of body), without subterminal sacs or bulbs but with variably developed lateral alae in some species, shaft dorsoventrally compressed over most of length, tapering gradually toward distal end (Fig. 1). Male palpal tibia with proximal ventral prominence with field of denticles, ventral surface concave in pro- or retrolateral view with coat of long, erect macrosetae, distal prolateral surface with row or field of denticles; prolateral tarsal denticles large, blunt-tipped, tightly packed, with row extending nearly full length of tarsus. Female genital operculum (Fig. 2) with deep transverse sulcus externally corresponding to internal transverse sclerotized phragma; phragma projecting dorsoposteriorly, forming a ventral space; ventral space divided by median septum; sternum (Fig. 3) typically with anterior median emargination and/or notch; posterior margin usually with median process projecting posteriorly into flexible cuticle of pregenital chamber.

Remarks.—The *calcar* species-group is monophyletic based on its unique reproductive morphology and unpublished results from molecular phylogenetic analysis (M. Burns, M. Hedin & J. Shultz, pers. comm.). The female genital operculum and sternum form an apparent pregenital barricade, with the anterior sternal margin projecting into the subphragmal space of the operculum and the median sternal notch engaging the median opercular septum. The sternal posterior process appears to act as a lever arm, with muscles extending to the base of the operculum rotating the

sternum and pressing it against the phragma. The barricade is frequently engaged in preserved specimens of *L. calcar* and *L. hoffmani* and may require unusual effort to open when dissecting the female genitalia. The presence of a female pregenital barricade suggests a role in excluding the penis during attempts at forced mating by males. Member species are limited to the central and eastern United States and adjacent southern Canada and its maritime provinces. We recognize four species: *L. nigropalpi* (Wood 1868), *L. calcar* (Wood 1868), *L. euserratipalpe* new species, and *L. hoffmani* new species.

KEY TO SPECIES OF THE *LEIOBUNUM CALCAR* SPECIES-GROUP

1. Male 2
   Female 5
2. Palpal femur with retrolateral denticles extending proximally, not limited to distal third (Fig. 10), retrolateral apophysis absent; penis narrowed at glans-shaft joint in dorsal perspective forming "neck" (Fig. 17) ..... *Leiobunum nigropalpi*
   Palpal femur with retrolateral denticles limited to distal third (Fig. 23, 37, 39, 51, 52), with retrolateral apophysis (Figs. 4, 37, 52, 54) or subterminal cluster of denticles (Fig. 23, 39); glans-shaft joint variable in dorsal perspective but without neck (Figs. 1, 31, 46, 61) 3
3. Penis shaft essentially straight, not curved in lateral perspective (Fig. 27), usually with a bilateral pair of small subterminal alae (Fig. 31); palpal femur with subterminal retrolateral cluster of sharp denticles, sometimes mounted on low mound; palpal femur gracile or slightly inflated distally, not strongly curved (Figs. 23, 24) ..... *Leiobunum euserratipalpe*
   Penis shaft strongly curved in lateral perspective (Figs. 42, 58), subterminal alae large to absent (e.g., Figs. 43, 46, 61); retrolateral apophysis present, varying from massive to small but rarely with a simple distal cluster of denticles; palpal femur inflated distally and usually strongly curved (Figs. 37–40, 52–55) 4
4. Penis bending dorsally in subterminal (alar) region in lateral perspective (Fig. 43), alae large to absent (Figs. 43, 46); penis length usually less than that of body (Fig. 43); widespread (Fig. 47) ..... *Leiobunum calcar*
   Penis shaft without subterminal dorsal bend or alae (Figs. 58, 61), penis length subequal to or longer than body (Fig. 58), northeastern North Carolina and southwestern Virginia (Fig. 47) ..... *Leiobunum hoffmani*
5. Sternum with short, weakly sclerotized posterior process distinct from the more sclerotized sternum (Fig. 15). . . *Leiobunum nigropalpi*
   Sternum without short, weakly sclerotized posterior process; process either absent (Fig. 29) or well sclerotized (Figs. 28, 44, 59) ... 6
6. Posterior process of sternum absent (Fig. 29) to less than half width of sternum (Fig. 28) ..... *Leiobunum euserratipalpe*
   Posterior process of sternum present and long, more than half the width of the sternum (Figs. 44, 59) 7
7. Palpal femur with retrolateral denticles enlarged distally, with some mounted on variably developed, low, rounded retrolateral apophysis (Fig. 41); anterior sternal notch usually shallow (Fig. 44) (rarely absent) but deep in large-bodied, southern montane populations (see Fig. 59); widespread (Fig. 47) ..... *Leiobunum calcar*
   Palpal femur with retrolateral denticles, sometimes larger distally but without retrolateral apophysis (Fig. 56); anterior sternal notch deep, U- shaped, extending to midpoint of the sternum body (Fig. 59); northeastern North Carolina and southwestern Virginia (Fig. 47) ..... *Leiobunum hoffmani*

Leiobunum nigropalpi (Wood 1868)
(Figs. 6–17)

Phalangium nigropalpi Wood 1868:22–23, figs. 3a–d.

Liobunum nigropalpi (Wood): Weed 1887:935; Weed 1889a:87–88; Weed 1892:187–188, pl. 4, figs. 1, 2; Banks 1893:211; Banks 1901:675; Roewer 1910:213–214; Roewer 1923:896–897.

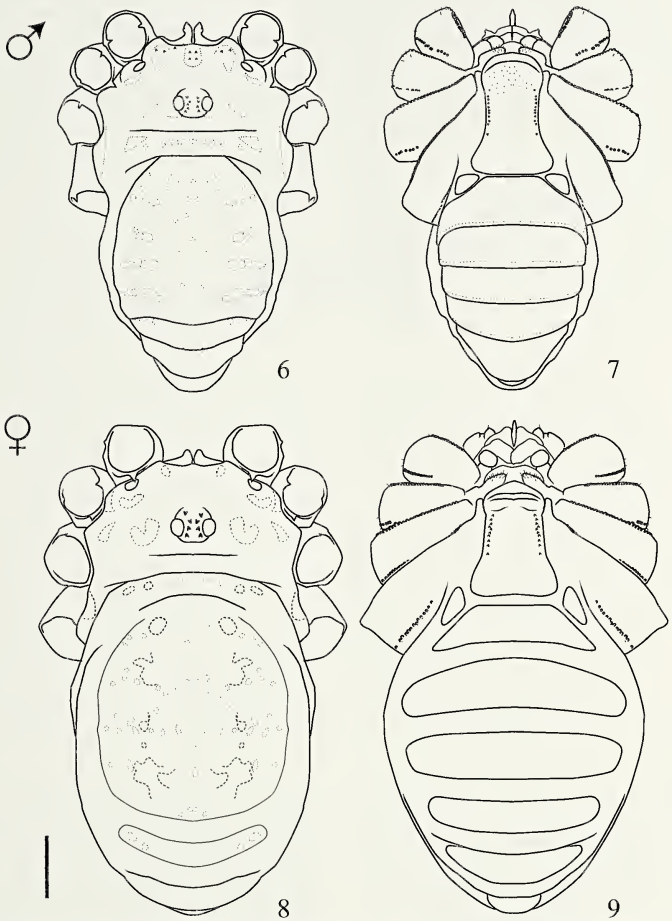
Liobunum nigripalpis (Wood): Weed 1890:918.

Leiobunum nigripalpi (Wood): Crosby & Bishop 1924:21; Walker 1928:163–164, pl. 2, fig. 14.

Leiobunum nigropalpi (Wood): Davis 1934:682–684, pl. 31, fig. 6; Bishop 1949:199–201, pl. 5, figs. 69–73; Edgar 1966:362; McGhee 1970:100, 106–113, figs. 21a, b, 24a, b, 26, 27 (unpublished dissertation).

Types examined.—*Phalangium nigropalpi*. Syntypes ♂ and ♀: USA: *Pennsylvania*: Huntingdon County (MCZ:14778).

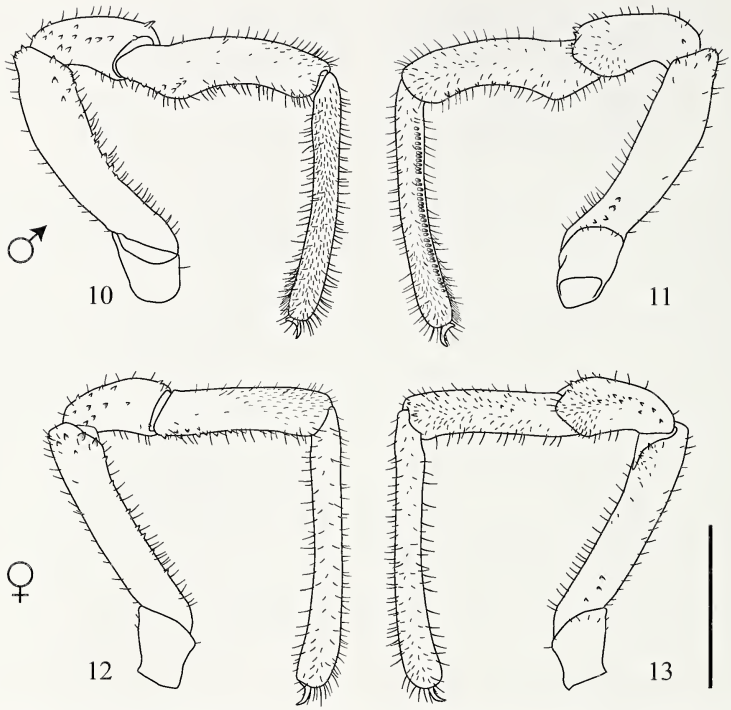
Other material examined.—USA: *Alabama*: Cleburne County: 2 ♂, Cheaha SP, vic. Campground #1 (046), 33.4864°N, 85.8125°W, 13 August 2005, M. Hedin et al. (UMD). *Connecticut*: Storrs County: 1 ♀, 41.8084°N, 72.2500°W, 28 July 1923, coll.? (AMNH). *Kentucky*: Bell County: 1 ♂, Pine Mt. State Park, "near lodge" 36.7357°N, 83.7375°W, 22 September 1963, Woods (AMNH). *Maryland*: Garrett County: 1 ♀, 3 km SE New Germany, Managed Oak Forest, 39.62°N, 79.105°W, elev. 779 m, 11–18 July 2005, M. Sarver; 2 ♀, 6 km NE Swanton, Managed Maple Forest, 39.489°N, 79.17°W, elev. 714 m, 21 June–6 July 2005, M. Sarver; 2 ♂, 4 ♀, 6 km NE Swanton, Managed Maple Forest, 39.489°N, 79.17°W, elev. 714 m, 22–29 August 2005, M. Sarver; 3 ♂, 4♀, 6 km NW Westernport, Old Growth Oak Forest, 39.509°N, 79.109°W, elev. 541 m, 3–10 August 2005, M. Sarver (UMD). *New York*: Cayuga County: 2 ♂, 2 ♀, N Fairhaven, 43.343°N, 76.6904°W, 31 July 1932, G. Hughes (AMNH). Ulster County: 1 ♂, 1 ♀, Cherrytown near Kerhonkson, 41.8251°N, 74.3293°W, 18 July 1976, Wygodzinsky (AMNH). *North Carolina*: Ashe County: 2 ♂, 1 ♀, 8.8 mi. [14.2 km] SSE Jefferson, 1183, 0.6 mi [1 km] N 1005, 36.29°N, 81.37°W, 21 July 1972, R.M. Shelley (NCMNS: 1217). Macon County: 3 ♂, 2 ♀, 5 mi [8.05 km] N of Highlands, 35.1269°N, 83.1924°W, August 1967, K. Kleinpeter (AMNH). Transylvania County: 1 ♀, 6.6 mi [10.6 km] WNW Brevard, Gov. Rd., 3.5 mi [5.6 km] W Fish Hatchery, 35.26°N, 82.85°W, 29 August 1973, R.M. Shelley (NCMNS: 1992). *Ohio*: Summit County: 2♂, 2 ♀, Bath Nature Preserve, 41.177°N, 81.642°W, 30 June 2005, J.W. Shultz (UMD). *Pennsylvania*: Bucks County: 1 ♀, Rushland, Wilkinson Rd., Coyne Farm, vernal marsh on wooded hilltop, 40.251°N, 75.038°W, 6–20 August 1998, H. O'Connor (ANSP). Huntington County: 1♂, 1♀, Huntington Mills, 41.1801°N, 76.2363°W, Woods (AMNH). Columbia



Figures 6–9.—Dorsal and ventral perspectives of *Leiobunum nigropalpi* (Wood 1868), male lectotype, female paralectotype. Scale bar = 1 mm.

County: 2 ♂, 2 ♀, Orangeville, 41.3392°N, 80.519°W, 13 August 1932, Hughes & Davis (AMNH). *South Carolina*: Oconee County: 2 ♂, Cherry Hill Rec. Area, Rt. 107, 34.9424°N, 83.0849°W, elev. 610 m, 11 August 1958, J.F. Hanson (AMNH). *Virginia*: Botetourt County: 2 ♀, Roaring Run, 37.6924°N, 79.8909°W, 4 July 1996, M. Donahue, B. Hogan (VMNH), 1 ♂, same locality, 30 July 1996, M. Donahue, B. Hogan (VMNH). Dickenson County: 1 ♂, 1 ♀, Breaks Interstate Park, "DF site 2, off Nature Trail," 37.2864°N, 82.2964°W, 15–29 June 1991, VMNH survey (VMNH), 1M, same locality, 22 August–6 October 1991, VMNH Survey (VMNH). Floyd County: 1 ♂, Buffalo Mountain Natural Area Preserve, trailhead at parking lot, 37.4316°N, 78.6569°W, elev. 1067 m, 20 June 2004, R.L. Hoffman (VMNH). 1 ♂, Buffalo Mountain, "ca 6 mi. [9.65 km] SE of Willis," 37.4316°N, 78.6569°W, elev. 1300 m, 25 August 1984, R.L. Hoffman (VMNH). Giles County: 4 ♂, Stony Creek Bog, off FS 10420, ca 2.3 km NW of Kire on Rt. 613, 37.4513°N, 80.5384°W, 9 August 2004, S.M. Roble (VMNH). Highland County: 1 ♂, Locust Spring Rec. Area, 8 mi [12.9 km] NW of Bluegrass, 38.5828°N, 79.6352°W, elev. 1158 m, 13 July 1974, Hoffman (VMNH). Russell County: 3 ♂, Mill Creek, ca 5.1 mi [8.2 km] E Carbo, 36.9432°N, 82.1386°W, late May 1998, J.C. Ludwig (VMNH). Wythe County: 1 ♂, 1 ♀, Sulphur Spring Picnic Area, ca 8 mi [12.9 km] west of Wytheville, 36.9692°N, 81.2222°W, 20 August 1967, Hoffman (VMNH).

Diagnosis.—Both sexes: Palpal femur, patella, and proximal tibia usually dark; distal tibia and tarsus light. Penis (Figs. 14,



Figures 10–13.—Palps of *Leiobunum nigropalpi* (Wood 1868), male lectotype, female paralectotype. Retrolateral perspectives on left, prolateral perspectives on right. Scale bar = 1 mm.

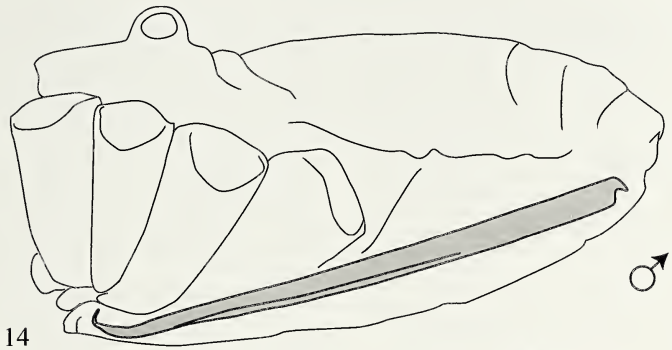
17): alae thin, translucent; shaft straight in lateral view, not widened or lobed proximally; glans-shaft union constricted transversely, glans broadened near base, tapering distally, terminating bluntly; glans held at slight dorsal angle to shaft; dorsal surface of glans with dorsal curvature. Male palp (Figs. 10, 11): femur without retrolateral apophysis; retrolateral denticles of femur distributed longitudinally, not restricted to distal field; tibia proximally with rounded-to-angular ventral prominence with field of short, stout denticles, especially proximally. Female sternum (Fig. 15): anterior margin with broad V-shaped median emargination with apex forming U-shaped notch; medial anterior margin reinforced by sclerotization; posterior margin with short, median process and weakly sclerotized cuticle.

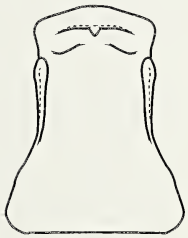
Description of male lectotype.—Body length: 5.6 mm. *Dorsum* (Fig. 6): Carapace length, width: 1.8 mm, 2.8 mm. Cuticle dark golden brown and finely granulate, lighter and smooth along meso- and metapeltidium posterior margin; transverse row of white dots extending across metapeltidium. Anteromedian preocular prominence slightly darker than surrounding cuticle, with a few small denticles scattered medially and extending along anterior carapace margin. Anterior process of supracheliceral lamina with a few small denticles dorsally. Ozopore mound smooth. Ocularium dark brown to black and canaliculate, each carina with 5 sharp denticles. Opisthosoma: Cuticle dark golden brown, lacking a central figure. Scutum finely granulate, scutal tergites demarcated by short lateral rows of sigilla and sparsely scattered white dots. Free tergites and anal operculum smooth.

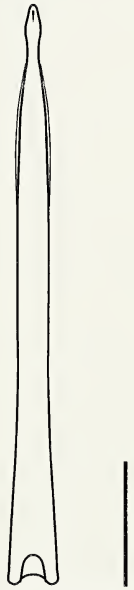
Venter (Fig. 7): Sternum simple. Labrum smooth, curved dorsally. Posterior margin of genital operculum and margin of sternites well demarcated, with anterior sternite overlapping posterior sternite. Cuticle dark golden brown, smooth, with short erect setae scattered on anterior genital operculum. Anterior lateral portions of operculum protruding slightly; anterior margin rebordered, white; small pointed denticles arranged in a row along medial lateral margin.

Penis (Figs. 14, 17): 4.2 mm long. Shaft straight, width constant throughout much of length but narrowing near junction with glans; glans curving slightly dorsad toward terminus. Alae, narrow, thin; ventral surface less sclerotized just posterior to glans; stylus missing but angled dorso-proximally in others.

Appendages: *Chelicerae*: Segments 1 and 2 pale yellow with a dorsal band of short, dark erect setae, becoming a dense prodistal patch near base of fixed finger.







Figures 14–17.—Genital structures of *Leiobunum nigropalpi* (Wood 1868): 14. Diagrammatic lateral perspective of male showing position of penis; 15. Ventral perspective of female sternum (genital operculum removed); 16. Dorsal (internal) perspective of female genital operculum; 17. Dorsal perspective of penis. All to same scale. Scale bar = 1 mm.

Palps (Figs. 10, 11): Measurements in mm: femur 1.7; patella 0.8; tibia 1.1; tarsus 1.4. Palpal segments dark brown, tarsus lighter. Trochanter medium brown with a few erect setae; distoventral apophysis with 1 or 2 denticles and setae. Femur slender, curved with slight distodorsal expansion; retrolateral apophysis absent; long proventral row of small, distally pointing denticles interspersed with erect setae; dorsal surface with scattered erect setae and a few distal, submarginal denticles; a few denticles form a short proximal prolateral row. Patella slightly expanded distally, with a distal prolateral apophysis coated with erect setae, setae continuing proximally as a dorsal row; field of scattered denticles cover the proximal retrolateral surface; one large denticle points distally on distodorsal margin. Tibia slender and slightly curved, forming a ventral concavity; proximodorsal surface slightly inflated; proximal ventral surface expanded, creating a flat prominence slightly more pronounced anteriorly than posteriorly, with a field of pointed denticles; other denticles arranged in a distal proventral row; erect setae cover the tibia (longer setae ventrally); distodorsal surface with coat of short recumbent setae. Tarsus slender, slightly inflated distally; tarsal denticles arranged in a tight proventral row; short recumbent setae and

long erect setae covering surface, setae longer ventrally, denser distally. Tarsal claw with 6 teeth.

Legs: Measurements of femur, patella, tibia, metatarsus, tarsus in mm: I: 8.7, 1.7, 7.1, 10.5, 11.1; II: 15.3, 1.7, 14.3, 14.3, missing; III: 8.2, 1.8, 7.5, 9.8, 11.7; IV: 11.8, 2.1, 9.8, 14.4, missing. Coxae smooth, concolorous with sternites; long, erect setae proximally. Anterior row of flat, evenly-spaced denticles developed along length of each coxa, terminating in distoventral submarginal row of small denticles and setae; proximal denticle row distal on coxae I, II, III, along full length of coxae IV. Trochanters reddish brown, with scattered distally-pointing denticles laterally. Femur divided into basal piece and shaft by a circumferential groove; cuticle dark brown, lighter distally; shaft with irregular rows of distally pointing denticles associated with a distal setae, denticles, and setae not developed on ventral surface, denticles especially numerous on legs I and III; a few denticles along distal margin, larger dorsally, and in short lateral rows basally. Patellae reddish brown, wider distally; small distally-pointing denticles with accompanying setae scattered over surface, sometimes arranged in loose rows, reduced ventrally; sharp denticles larger on distal dorsal margin, smaller on ventral margin. Tibiae golden brown with a coat of fine recumbent setae, denser distally; scattered denticles with accompanying setae, some forming 4 or 5 rows, denser proximally and dorsally; proximal dorsal margin with rounded median process; distal margin with ventral row of pointed denticles terminating with lateral spines. Tibia II with reduced denticles, vestiture of microtrichia, 4 incomplete pseudoarticulations, and about 30 partial circumferential rings. Metatarsi golden brown with a coat of recumbent setae; Legs I and III with 3 pseudoarticulations, leg II with 9, leg IV with 5, each pseudoarticulation with a ventral pair of distally-pointing spines. Tarsi golden brown, distal-dorsal margin of each segment dark; longer segments each with ventral pair of spines; recumbent setae cover entire cuticle, setae denser, longer ventrally and distally.

Variation in male.—*Leiobunum nigropalpi* shows comparatively little variation. Most are yellowish ventrally and golden to orange-brown dorsally with medium to dark brown legs, but some are lighter in color, with a white ventral surface, pale yellow dorsal surface, or golden-brown legs. Tibial denticles of the palp and posterior coxal denticle rows may be reduced or absent. The proximo-ventral prominence of the palpal tibia usually flat, but occasionally with the distal portion projecting ventrad, forming a small spur.

Description of female paralectotype.—Body length: 7.3 mm. *Dorsum* (Fig. 8): Carapace length, width: 2.1 mm, 2.9 mm. Cuticle brown, coarsely granulate with a few pointed denticles on mound of ozopore; ocularium nearly black, strongly canaliculate, each carina with 5 curved denticles. Supracheliceral lamina smooth. Opisthosoma: Generally brown with a weak central figure indicated by irregular dark bordering with dark anterior blotches on tergite 1 and a dark medial region of tergite 4; cuticle coarsely granular anterior, smoother posterior. Tergites 1–5 (scutum) demarcated by bands of whitish dots; remaining tergites appear somewhat reduced and separated from scutum (possibly due to swelling during preservation); tergite 8 and anal operculum granulate, anal operculum with a few small denticles.

Venter (Fig. 9): Labrum straight, smooth. Sternites finely granulate, dark golden brown, anterior half of each sternite with a lighter transverse band that terminates before lateral margins. Posterior margin of genital operculum and margins of sternites distinct. Genital operculum dark golden brown, lighter medially; dark denticles and setae form a longitudinal band, more numerous anteriorly; anterior body slightly bilobed with lobes protruding ventrad; margin thickly rebordered, white, protruding medially; a transverse sulcus with corresponding inner (dorsal) phragma developed between bilobed body and rebordering; phragma thicker and more prominent medially; small anterior-pointing apophyses developed on anterior lateral margins corresponding to the position of the sternum; sternum dark, nearly black medially around a broad v-shaped emargination; shoulders angled rather than square as in the other species in the group, median posterior process tiny, with tendons attached along posterior sternite margin.

Appendages: *Chelicerae*: Cuticle golden, basal article with short erect setae sparsely scattered on dorsal surface (denser distally), extending to distal dorsal and prolateral surfaces of second article; setae especially dense around the base of the fixed finger.

Palps (Figs. 12, 13): Measurements in mm: femur 1.7; patella 0.6; tibia 0.9; tarsus 1.5. Cuticle golden to golden brown. Trochanter with a few scattered denticles and setae distoventrally. Femur expanded distally with 4 or 5 denticles in a proximal prolateral row; pointed dentieles arranged in a retroventral row and extending along the distal-dorsal margin, long erect setae interspersed and forming a proventral row, a few scattered dorsally. Patella with distal prolateral apophysis densely covered in long erect setae; pointed denticles extend along distal dorsal margin and form prodorsal and retrodorsal bands, each interspersed with a row of long erect setae. Tibia ventral surface slightly curved, with a few distally pointing denticles in a loose proximal row; fine recumbent setae and long erect setae cover surface. Tarsus expanded distally; surface with a coat of fine recumbent setae, long erect setae in irregular rows; setae dense and longer distoventrally, especially around tarsal claw. Claw with six teeth.

Legs: Measurements of femur, patella, tibia, metatarsus, tarsus in mm: I: 7.7, 1.9, 6.0, 8.1, 10.2; II: 13.4, 1.7, missing, 12.3, 12.5; III: 7.3, 1.2, 5.9, 8.9, 10.2; IV: 11.0, 1.1, 8.4, 12.5, 14.9. Coxae dark golden brown, smooth, with sparse scattered setae. Large, flat denticles developed in a prolateral and retrolateral row on each coxa; tiny rounded denticles present submarginally; all prolateral rows and coxa IV retrolateral row extends full length of coxa (or nearly so); retrolateral rows of coxae I–III extend over half the length of the coxa; prolateral dorsal surface of coxa III and retrolateral dorsal surface of coxae I and II slightly protuberant; coxae I and II with a single dark tubercle. Trochanters smooth ventrally; dorsal surface with medial groove; distally-pointing denticles developed on lateral surfaces. Femur proximally reddish-brown, distally lighter; divided into basal piece and shaft by circumferential groove. Distally-pointing denticles scattered on basal piece and in 7–12 irregular rows down the shaft, most with accompanying distal erect setae; ventral surface smooth; two large denticles present on distal-dorsal margin. Patellae distal dorsal surface expanded, with 4 longitudinal rows of denticles, larger distally; distal ventral margin with a few distally-pointing denticles. Tibiae golden with vestiture of

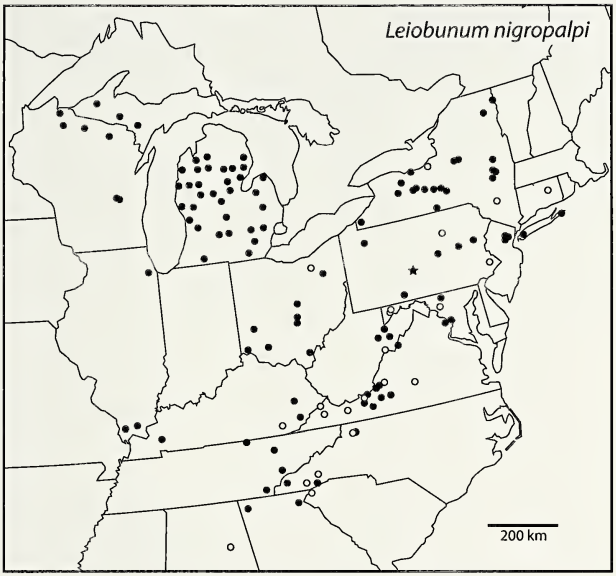


Figure 18.—Map of collection localities for *Leiobunum nigropalpi*. Open circles are localities of specimens observed in this study. Black circles are localities obtained from the literature (Bishop 1949; Davis 1934; Edgar 1971; Levi & Levi ; McGhee 1970; Weed 1892). A star indicates the type locality.

microtrichia and a coat of recumbent setae; proximal surface with 4 rows of denticles; dorsal margin with a few denticles and a small process. Left tibia II with 4 incomplete pseudoarticulations, right tibia II with 7, and both with numerous faint circumferential rings. Metatarsi golden with a coat of recumbent setae; a few scattered denticles proximal; erect setae form a few sparse rows; 5 pseudoarticulations on metatarsi I, III, and IV, 7 on II, each with ventral pair of spines and sometimes a dark dorsal spot. Telotarsi golden with a few rows of sparse erect setae and a coat of dark recumbent setae, denser distally and ventrally on each segment, especially distal segments; longer (proximal) segments with a pair of ventral submarginal spines. Tarsal claw smooth.

Ovipositor: Damaged, but two spermathecae visible between rings 4 and 5; otherwise typical: shaft dorsoventrally flattened; width constant to base of furca; anterior rings each with a transverse row of 2–10 erect setae (denser distally) on dorsal and ventral surfaces; furca lightly sclerotized, tapered anteriorly, and constricted at base; surface with many long setae; terminal sense organs anterior-lateral.

Variation in female.—As in males, there is little variation. The anterior genital operculum may be bilobed or straight, with or without anterior-lateral protuberance. The central figure, white spots, and sigilla color vary in intensity. Pro- and retrolateral rows of denticles may be reduced or absent on coxae II and III.

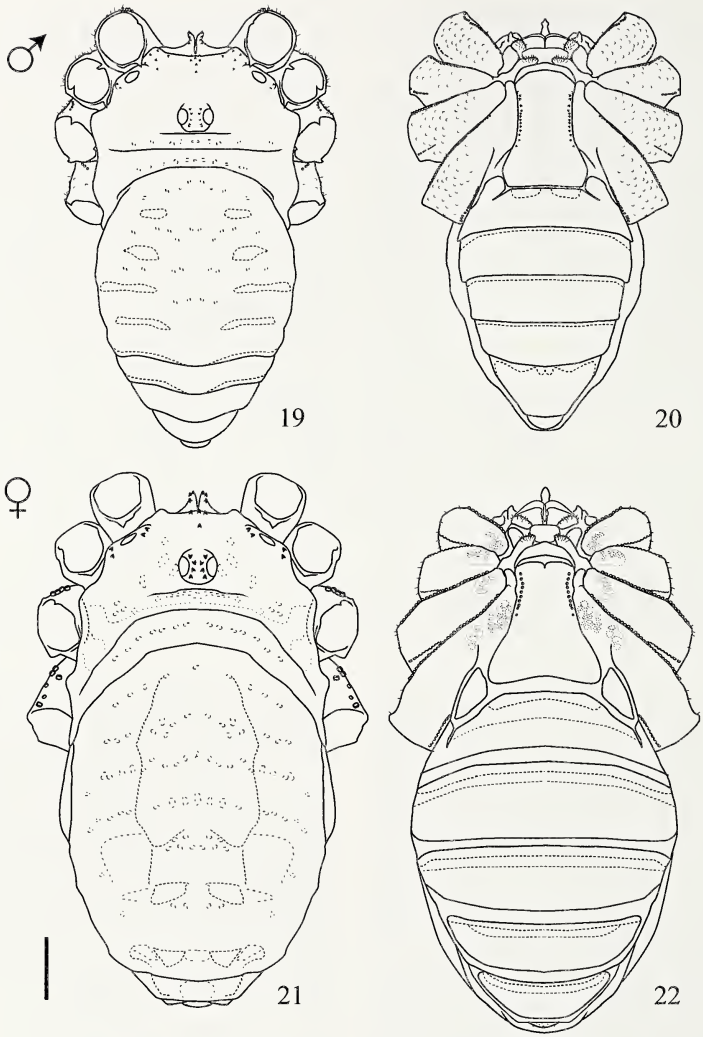
Range.—Forests of the eastern United States and, perhaps, southeastern Canada (Fig. 18).

Remarks.—*Leiobunum nigropalpi* is morphologically uniform throughout its range and many of its features are plesiomorphic relative to other members of the species-group based on outgroup comparision with closely related North American species (e.g., *L. politum* Weed 1890, *L. aldrichi* Weed 1893, *L. verrucosum* (Wood 1870), *L. ventricosum* (Wood 1870), *L. vittatum* species-group) (M. Burns, M. Hedin, J. Shultz., unpublished molecular phylogeny). Specifically, the male palps are generally gracile, with the retrolateral denticles of the femur occurring in a long longitudinal series, rather than being restricted to a distal region, and a retrolateral femoral apophysis is absent. Furthermore, the penis narrows at the glans-shaft junction, as in species with primitive sacculate penes, and the posterior process of the female sternum is only lightly sclerotized.

Leiobunum euserratipalpe new species
(Figs. 19–31)

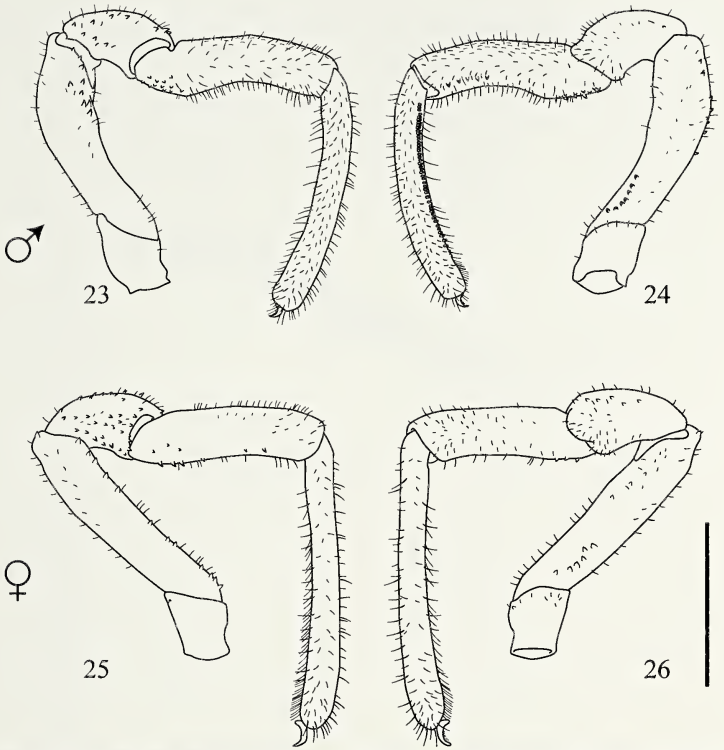
Leiobunum serratipalpe Roewer 1910: Davis 1934:689–690, pl. 31, figs. 3, 4, pl. 33, fig. 32; Bishop 1949:203–204, pl. 6, figs. 80–83; Edgar 1966:363, fig. 7; McGhee 1970:114–121, figs. 21c, d, 24c, 28, 29 (unpublished dissertation) (all misidentifications).

Types examined.—Holotype: USA: *Virginia*: Prince William County, Manassas National Battlefield Park, ~0.3 km S of Sudley Spring, 38.8168°N, 77.5164°W, 22 July 1999, A.C. Chazal (NMNH). Paratype: 1 ♀, collected with holotype (NMNH).



Figures 19–22.—Dorsal and ventral perspectives of *Leiobunum euserratipalpe* new species, male holotype, female paratype. Scale bar = 1 mm.

Other material examined.—USA: *Maryland*: Howard County: 3 ♂, 2 ♀, Middle Patuxent Environmental Area, 39.2056°N, 76.9081°W, 27 July 2007, R. Smith (UMD). Montgomery County: many ♂ and ♀, Upper Seneca Crest, 32.2575°N, 77.1735°W, Summer 2010, J.W. Shultz (UMD). *Michigan*: Livingston County: 2 ♂, George Reserve, 42.4667°N, 84.0000°W, 18 July 1936, I.J. Cantrall (AMNH). *Mississippi*: Lafayette County: 2 ♀, 1 mi [1.61 km] SW Abbeville, in deciduous woods on low vegetation, 34.489°N, 89.510°W, 10 July 2008, P. Miller (UMD), 1 ♂, same locality, 25 May 2008, P. Miller, G. Stratton (UMD). *North Carolina*: Graham County: 1 ♂, Joyce Kilmer Memorial Forest, 35.374°N, 83.975°W, 26 June 1977, W. Shear (VMNH). Jackson County: 1 ♂, 1 ♀, 7.3 mi [11.7 km] SSE Cashiers, 1177, 0.1 mi [0.16 km] N South Carolina state line, 35.019°N, 83.060°W, 28 August 1973, R.M. Shelley (NCMNS: 1944). Wake County: 1 ♀, Umstead Park, 35.859°N, 78.750°W, 12 September 1973, R.M. Shelley (NCMNS: 2023). Person County: 1 ♂, 8.4 mi

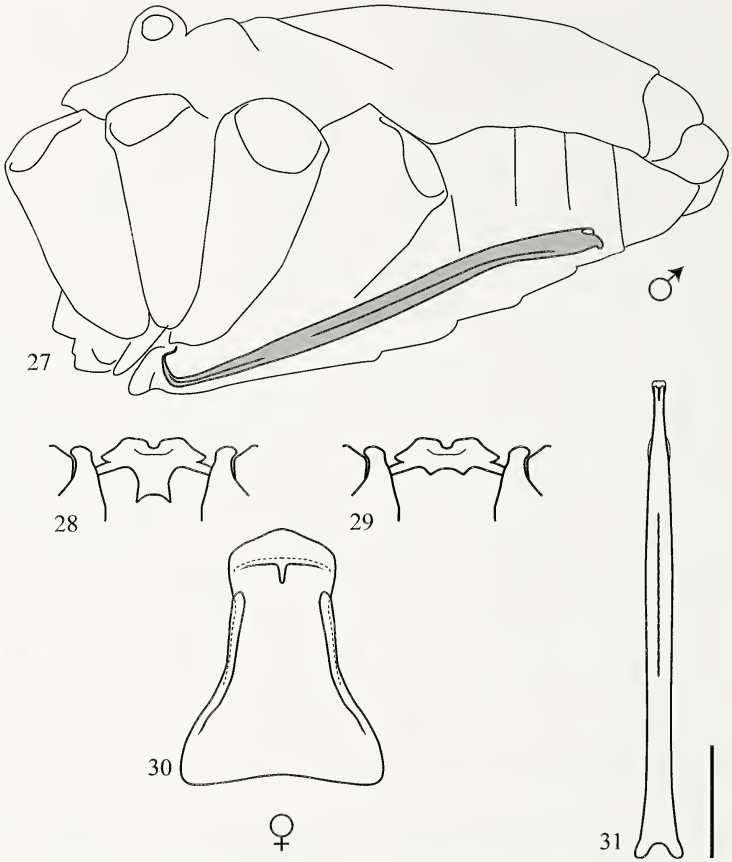


Figures 23–26.—Palps of *Leiobunum euserratipalpe* new species, male holotype, female paratype. Retrolateral perspectives on left, prolateral perspectives on right. Scale bar = 1 mm.

[13.5 km] NW Roxboro, 1392, 0.4 mi [0.64 km] E 1300, 36.45°N, 79.12°W, 18 July 1973, R.M. Shelley (NCMNS: 1824). *Ohio*: Hocking County: 2 ♂, Clear Creek Twp, 39.5406°N, 82.7356°W, 10 September 1931, T.H. Hubbell (AMNH). *Pennsylvania*: Bucks County: 2 ♂, 2 ♀, Rushland, Wilkinson Rd., Coyne Farm, vernal marsh on wooded hilltop, 40.250°N, 75.042°W, 6–20 August 1998, H. O'Connor (ANSP); many ♂ and ♀, same locality, 21 July–5 August 1998, H.O 'Connor (ANSP). Cumberland County: 1♀, Boiling Springs, 40.1498°N, 77.1283°W, 8 August 2010, J. Ryndock (MEM). *Virginia*: Clarke County: 5 ♂, Blandy Farm, ca 3 mi [4.8 km] south of Boyce, 39.0624°N, 78.0622°W, 1 August 1991, D.R. Smith (VMNH). Cumberland County: 2 ♂, "Hardwood site 1 (north)" 2 km SSW of Columbia, 37.732°N, 78.175°W, 1 August 1990, J.C. Mitchell (VMNH). Essex County: 4 ♂, 1 ♀, 1.5 km SE Dunnsville, "Malaise trap B1#1", 37.8473°N, 76.8015°W, 12 July 1991, D.R. Smith (VMNH). Fluvanna County: 6 ♂, 2 ♀, Kents Store, Bell drift fence site, 37.8779°N, 78.1286°W, 13 September 1995, M. Bell (VMNH). Henrico County: 1 ♂, Westhampton, west Richmond, 37.5741°N, 77.5146°W, June–July 1991, W. Mitchell (VMNH); 1 ♀, National Guard Facility, 2 mi [3.2 km] SE of Sandston on LaFrance Rd., 37.498°N, 77.292°W, 11 July–19 August 2001, K.L. Derge (VMNH). Henry County: 1 ♂, Broeski's Farm, ca 2 mi [3.2 km] E of Sandy Level in pitfall traps, 36.571°N, 79.681°W, 22 August–18 September 1987, RLH (VMNH); 1 ♂, 1 ♀, Vicinity of Martinsville, 36.692°N, 79.865°W, 4 August 1993, Career Club Excurs. (VMNH). Isle of Wight County: 2 ♂, Zuni Pine Barrens, 36.7803°N, 76.8914°W, 31 August [?], C.A. Pague (VMNH). Prince William County: 1 ♂, 1 ♀, Manassas NBP, 0.3 km S of Sudley Spring, 38.8168°N, 77.5164°W, 22 July 1999, A.C. Chazal (VMNH). York County: 3 ♂, 1 ♀, Cheatham Annex Naval Supply Base, "Cheatham Pond DF site", 37.2934°N, 76.619°W, 6 July 1989, DNH survey (VMNH).

Etymology.—The specific epithet means "true" *serratipalpe*. The name reinforces the distinctiveness of the species from the type of *L. serratipalpe* Roewer 1910, which Cokendolpher (1981) showed to be a female *L. calcar*, while acknowledging the later and more accurate concept of *L. serratipalpe* as developed by American workers (Davis 1934; Bishop 1949; Edgar 1966; McGhee 1970). See "Remarks" for details.

Diagnosis.—Penis (Figs. 27, 31): shaft essentially straight in lateral view, usually with a pair of small, subterminal alae;



Figures 27–31.—Genital structures of *Leiobunum euserratipalpe* new species: 27. Diagrammatic lateral perspective of male showing position of penis; 28, 29. Ventral perspective of typical variants of female sternum (genital operculum removed); 30. Dorsal (internal) perspective of typical female genital operculum; 31. Dorsal perspective of penis. All to same scale. Scale bar = 1 mm.

glans-shaft junction not demarcated dorsally, no constriction from dorsal or lateral view, glans tapering distally, with strong dorsal curvature. Male palps (Figs. 23, 24): generally gracile; femur inflated somewhat distally, with very low retrolateral apophysis or none, but with retrodistal field of large denticles; retrolateral armature limited to distal 1/3 of femur; tibia inflated ventroproximal forming a rounded-to-flat prominence with field of denticles. Female: sternum usually with small median anterior notch (sometimes absent) and with small (less than half sternum width) posterior median process (Figs. 28, 29), palpal femur lacking retrolateral apophysis (Fig. 25). Both sexes with a long prolateral row of denticles extending the full length, or nearly so, of each coxa.

Description of male holotype.—Body length: 6.3 mm. *Dorsum* (Fig. 19): Carapace length, width: 1.7 mm, 2.8 mm. Cuticle coarsely granulate, golden brown with dark sigilla lateral to ocularium. Supracheliceral lamina parallel with tips diverging, a few large denticles form a row down dorsal surface of each side. Median preocular prominence with 6 denticles in 2 transverse rows. Ozopore white, ringed in brown. Sharp denticles circling ozopore and scattered between mound and median prominence. Ocularium dark brown, lighter medially, weakly canaliculate; 7 denticles on left carina, 8 denticles on right carina. Mesopeltidium slightly elevated above surface of propeltidium; mesopeltidium and metapeltidium each with transverse row of white spots. Opisthosoma: Tapered posteriorly; cuticle golden brown, coarsely granulate, covered in tiny tubercles. Scutal tergites (tergites 1–5) distinguished by transverse, lateral rows of sigilla and bands of white dots; posterior margins of tergites 5 and 6 rebordered

medially, straight, brown; lateral margin of dorsum white, especially on posterior tergites. Anal operculum golden brown with small scattered denticles.

Venter (Fig. 20): Labrum with slight dorsal curvature and a subterminal pair of small lateral tubercles. Sternites golden brown, darker anteriorly; cuticle finely granulate. Posterior margin of sternites 3–5 straight; sternite 7 trapezoidal. Two large sigilla extend from the posterolateral genital operculum to the anterior margin of sternite 3. Sternite 3 and lateral sternite 2 partially fused, genital operculum clearly demarcated. Operculum golden brown with lateral submarginal rows of pointed denticles and small scattered denticles and erect setae; anterior margin rebordered, white.

Appendages: *Chelicerae*: Golden brown with short darker bands on proximal prodorsal and retrodorsal surfaces of second article. Distodorsal surface of first article and dorsal and prolateral surfaces of seeond with scattered erect setae, denser on distal prolateral surface.

Palps (Figs. 23, 24): Measurements in mm: femur 1.5; patella 0.7; tibia 1.2; tarsus 1.5. Primarily golden brown, dorsal femora surface with incomplete brown bands. Trochanter with 3 distal denticles and prolateral submarginal row of erect setae. Femur arched distally with a small distal retroventral process; large, dark, distally-pointing denticles clustered on the anterior surface of the process, a few scattered distally; distodorsal surface with 2–3 irregular rows of denticles; proximal prolateral surface with a row of 7 dark, blunt denticles on left femur, 9 on the right; setae scattered on dorsal, ventral, and distal prolateral surfaces. Patella with submarginal row of dark distally-pointing denticles and erect setae, interrupted ventrally; a few smaller denticles scattered on surface; distal prolateral margin protuberant with a coat of erect setae. Tibia slightly curved, forming a shallow ventral concavity; proximal ventral surface expanded, forming a square, flat region covered with small, dark proximally-pointing denticles (retrolateral denticles smaller and pointing distally); proximodorsal surface slightly inflated; distal proventral surface with longitudinal row of 5 evenly spaced, dark-tipped denticles; entire surface with a coat of long erect setae, fine recumbent setae present dorsally. Tarsus slightly arched and curving slightly prolaterally; surface coated with long erect and short recumbent setae; dark blunt denticles arranged in a tight row down the length of the proventral surface, with denticles at either end smaller and pointed; distal ventral tip with dense, fine erect setae. Tarsal claw with 5 distally pointing teeth increasing in length distally.

Legs: Measurements of femur, patella, tibia, metatarsus, tarsus in mm: I: 7.8, 1.6, 6.4, 8.4, 10.8; II: 13.5, 1.6, 12.7, 12.9, 28.3; III: 7.3, 1.6, 5.9, 8.9, 11.1; IV: 10.3, 1.9, 7.1, 8.6, 10.8. Coxae golden brown, slightly lighter, and mottled proximally; short erect setae and rounded denticles scattered over surface; large sharp denticles (some pointed, some flat-topped) arranged in a tight row down the anterior length of all coxae; coxa IV with complete posterior row, distal end of anterior row curving dorsally, adjacent to margin of coxa III, with smaller denticles scattered distally; coxae I, II, and III with a short, distal retrolateral row of denticles. Trochanters dark reddish-brown; small pointed denticles scattered over all but the ventral surface, increasing in size dorsally; small denticles arranged in a distal ventral submarginal row; denticles larger on trochanter I, smaller on trochanter IV. Femur basal piece defined by circumferential ring, concolorous with trochanters; row of small distally-pointing denticles circle the basal piece, larger dorsad; ventrally-pointing projection on proximal ventral margin; shaft golden brown with dark-tipped distally-pointing denticles arranged in loose longitudinal rows, prolateral and retrolateral denticles smaller and denser; femora I, III, and IV wider distally with a ventral submarginal row of denticles. Patellae golden with reddish-brown mottling; dorsal surface slightly arched distally; large sharp denticles arranged in a distal submarginal row, smaller denticles and setae arranged in a few longitudinal rows (reduced on patella II). Tibiae golden brown with dark flecks and blotches, leg II lighter; denticles with distally adjacent setae scattered over surface and forming a distoventral submarginal row; fine recumbent setae present; all denticles reduced on tibia II, but 5 rows of erect setae and 5–7 incomplete pseudoarticulations present. Metatarsi golden with a coat of fine recumbent setae and 5 rows of erect setae; 5 incomplete pseudoarticulations each with a ventral pair of spines on distal half of metatarsi I, III, and IV, 7 pseudoarticulations with reduced spines on metatarsus II. Tarsus with 5 rows of erect setae; ventral spines present only on proximal (longer) segments; fine erect setae on ventral surface, denser on the distal segments, longer setae clustered ventrally and dorsally around the tarsal claw. Tarsal claw curved, reddish, smooth.

Penis (Figs. 27, 31): 4.2 mm. Shaft without sacs or bulbs, but with a pair of small, subterminal alae; shaft straight with a slight ventral curve at base; shaft somewhat dorsoventrally flattened, rounder medially, tapers distally; no distinct joint present between the shaft and glans; glans narrow and eurving dorsally at a 90° angle, slightly expanded laterally at curve; stylus projecting slightly posterior.

Variation in male.—Labrum may be straight or sharply curved dorsally. Size and number of denticles on the palpal tibia varies. Cuticle surface texture ranges from smooth to very coarse. Penis shaft usually straight, but infrequently curved dorsally; glans usually strongly curved, but may be less so, frequently due to preservation (distinguished by a wrinkled patch of cuticle on the ventral surface of the curve). Small alae absent or present, sometimes extending over curve of glans. Leg color ranges from golden to dark brown. Sternite 2 may or may not be distinct from genital operculum.

Description of female paratype.—Body length: 7.9 mm. *Dorsum* (Fig. 21): Carapace length, width: 2.1 mm, 3.4 mm. Cuticle covered with tiny scattered tubereles creating a coarsely granular texture; tubercles dark and more prominent on medial mesopeltidium and metapeltidium. Anteromedian prominence with three rows (1 median and 2 lateral) of 2–3 denticles. Ozopore mound with a few denticles scattered on each side. Ocularium weakly canaliculate with 5 pointed denticles and a few scattered erect setae on each carina; dark reddish-brown, darker around the eyes. Propeltidium golden brown, darker anterior to ocularium, with dark lateral sigilla and marginal border near leg III. Mesopeltidium and metapeltidium each with reddish-brown medial band, whitish posterior and lateral margins, gold anterior margins, and white lateral spots. Supracheliceral lamina golden brown with an irregular row of pointed denticles on dorsal and anterior surfaces of each parallel side. Opisthosoma: Abdomen oval and slightly tapered posterior; cuticle coarsely granular and

predominantly medium-reddish brown, darker laterally; tergites 1–6 form a scutum, with each tergite distinguished by color; faint central figure indicated by dark border; bordering breaks up at tergite 4, becoming two anterior dark blotches on tergites 5–7; transverse bands of white dots extend across tergites 1–3, limited to lateral regions of the posterior tergites; tergites 5–7 light in color lateral to the central figure, appearing as 2 large posterior white blotches from a distance. Anal operculum golden reddish-brown with a few tiny scattered erect setae.

Venter (Fig. 22): Labrum straight with pair of small subterminal lateral tubercles. Sternites golden reddish-brown with a lighter anterior transverse band, darker anterior margin, and white posterior and lateral margins; surface smooth with short, scattered erect setae. Genital operculum golden brown with two posterolateral sigilla; cuticle smooth with a few scattered erect setae. Genital operculum and sternites well demarcated. Flat-topped denticles arranged in a lateral submarginal row (smaller posteriorly) on anterior half of the operculum. Anterior margin thickly rebordered and protruding anteriomedially, forming a thick white "lip" with posterior sulcus; a very short medial sulcus extends posteriorly from transverse sulcus. Inner (dorsal) surface (Fig. 30) with posterior-pointing "shelf" (phragma) and median septum, corresponding to the external sulci. Sternum (Fig. 28) straight and thick, with a small medial notch; posterior margin with rectangular median process about half the width of the sternum, muscles attached to the dorsal (inner) surface of the process.

Appendages: *Chelicerae*: Golden brown with scattered erect setae on dorsal surfaces of first and second article; second article with narrow prolateral distal band of erect setae becoming a dense cluster just proximal to fixed finger.

Palps (Figs. 25, 26): Measurements in mm: femur 1.5; patella 0.7; tibia 1.2; tarsus 1.8. Palpal segments uniformly golden brown. Trochanter with 2 tiny submarginal distally-pointing retrodorsal and ventral denticles; setae form a distal prodorsal field and sparse, ventral submarginal row. Femur narrow, slightly wider distally; small distally pointing denticles arranged in a retroventral row terminating at a distal submarginal row, setae interspersed, denticles denser distally, setae denser proximally; weak proventral row diverging; proximal prolateral surface with a row of 7 denticles on left femur, 6 on right femur, and scattered erect setae; distal dorsal and prolateral margin each with one denticle, surfaces with erect setae arranged in a few irregular rows. Patella with a rounded distal prolateral apophysis; coat of short, erect setae covers process, distal ventral, and prolateral surfaces; prodorsal, retrodorsal, and retrolateral surfaces each with a wide longitudinal band of scattered distally-pointing denticles and setae; a distal submarginal row of denticles interrupted at process. Tibia with a coat of fine, dark recumbent setae on all but the ventral surface; erect setae scattered ventrally and forming loose rows dorsally; denticles scattered on the retrolateral surface and form a distal irregular pro- and retrolateral row; 2 denticles on distal prolateral margin. Tarsus with a coat of recumbent setae and 6–8 loose rows of erect setae (denser and finer distally, particularly around the tarsal claw). Tarsal claw reddish-brown, darker distally, with 7 teeth.

Legs: Measurements of femur, patella, tibia, metatarsus, tarsus in mm: I: 8.4, 1.7, 6.7, 8.3, 11.0; II: 15.5, 1.9, 14.0, 13.4, 29.7; III: 8.3, 1.6, 6.4, 8.9, 11.6; IV: 12.5, 2.0, 9.3, 13.9, 17.4. Coxae light reddish to golden brown, slightly lighter and mottled proximally; short erect setae and tiny rounded denticles sparsely scattered over surface and arranged in a ventral submarginal row; tight rows of flat-topped denticles extend nearly the full length of the prolateral and retrolateral surfaces, with prolateral denticles larger on coxae I, II, and III, and retrolateral denticles larger on coxa IV; coxa IV extends beyond the margin of coxa III, exposing the distal anterior-dorsal surface; a few small scattered denticles and 2 larger submarginal denticles present in the exposed region. Trochanters dark reddish-brown, pointed denticles scattered pro- and retrolaterally and arranged in a distal ventral submarginal row with a few interspersed erect setae; denticles larger on trochanter I, smaller on trochanter IV. Femora basal portion dark reddish-brown with a row of small denticles circling distally, interrupted ventrally; shaft golden brown and slightly expanded distally (except femur II); 6–7 loose rows of distally-pointing denticles and distally-adjacent seta on all but the ventral surface, dorsal denticles larger; two large submarginal distally-pointing denticles present dorsally and 3 smaller denticles pro- and retrolaterally; femur II denticles reduced. Patellae golden brown with darker dorsal mottling; small distally-pointing denticles in 4–6 loose longitudinal rows and in a distal submarginal row, dorsal denticles larger; denticles reduced on patella II. Tibiae golden brown with a coat of fine recumbent setae and 5 longitudinal rows of erect setae and small proximal denticles; distal margin dark with proventral and retroventral rows of small denticles, each terminating with a dark spine; tibia II mostly lacking denticles, but retaining ventrolateral spines; 5–6 incomplete pseudoarticulations on tibia II; vestiture of microtrichia present distally on all tibia. Metatarsi golden brown, distal margin reddish; cuticle with a coat of recumbent setae and 5–7 rows of short erect setae; 4–5 faint pseudoarticulations (11–12 on metatarsus II) indicated by a reddish dorsal mark, each with a pair of distally-pointing ventral spines (absent from some pseudoarticulations on metatarsus II). Tarsus golden brown, darker distally, proximal half of first segment and dorsal distal margins of all segments darker; a pair of spines present at the distal ventral margin of all but the most distal segments; recumbent setae cover entire surface, denser and longer ventrally and distally; short erect setae arranged in 5–7 rows down the length of the tarsus, longer erect setae clustered around tarsal claw. Tarsal claw reddish.

Ovipositor: Typical; two spermathecae visible in ring 6, shaft slightly expanded dorsoventrally around the spermathecae.

Variation in female.—The sternal notch is reduced in a few specimens we have seen, and the posterior sternal process is absent in specimens from eastern Pennsylvania, Maryland and northeastern Virginia. However, it is likely that the sternal process sclerotizes during the adult instar; in populations with sternal processes, it is variably expressed in early-season (June) individuals but is present and well sclerotized in specimens collected in August and September. Therefore, the collection date should be taken into consideration when identifying females that may belong to this species. Intensity of dorsal color, pattern, and central figure varies greatly, but posterior whitish blotches on the opisthosoma are usually visible. Leg

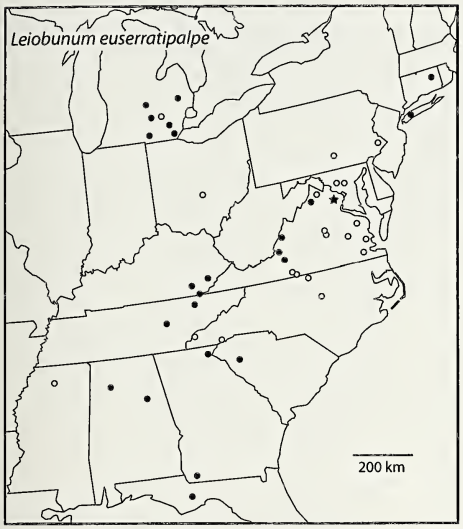


Figure 32.—Map of collection localites for *Leiobunum euserratipalpe* new species. Open circles are localities of specimens observed in this study. Black circles are localities obtained from the literature (Bishop 1949; Davis 1934; Edgar 1971; McGhee 1970). A star indicates the type locality.

color ranges from golden to dark brown. Denticles of the palpal tibia sometimes reduced.

Range.—This species is widely distributed east of the Mississippi River and is common in the Atlantic Coastal Plains and Piedmont of the eastern United States (Fig. 32).

Remarks.—Although it is technically a new species, *L. euserratipalpe* already has a complicated taxonomic history. *Leiobunum serratipalpe* Roewer 1910 was described from specimens collected in "Long Lake" and "Cold River, North America." Cokendolpher (1981) examined the "male" cotype (the only specimen that appears to be available) and found it be an adult female *L. calcar,* an observation that we have confirmed. Without reference to the type material, Crosby & Bishop (1924) questioned the validity of *L. serratipalpe* and speculated that purported male specimens were actually subadult males of *L. calcar*. In addition, no confirmed adult female *L. serratipalpe* had been described (but see McGhee 1970), although it was assumed to closely resemble female *L. calcar*. Cokendolpher (1981) found several *L. serratipalpe*-like specimens within a large collection of *L. calcar* from Maine, USA, and concluded that *L. serratipalpe* was a junior synonym of *L. calcar*. This verdict was widely accepted, and *L. serratipalpe* was subsequently omitted from checklists and keys of North American harvestmen (e.g., Edgar 1990) and its records were lumped with those of *L. calcar* (e.g., Cokendolpher & Lee 1993).

However, one of the most common summer species in the Mid-Atlantic Coastal Plain and Piedmont of Pennsylvania, Maryland and Virginia (named here *L. euserratipalpe*) corresponds to the traditional descriptions of *L. serratipalpe* (e.g., Davis 1934; Bishop 1949; Edgar 1966; McGhee 1970). *Leiobunum calcar* is largely absent from this region but is common in the adjacent Appalachian Mountains. The two species are sometimes found together, but they are readily distinguished by size and reproductive structures. *Leiobunum euserratipalpe* also occurs in the southern portion of the United States (e.g., Mississippi), again where *L. calcar* is absent. Although it is clear that *L. euserratipalpe* is distinct from *L. calcar* in the regions cited above, it is premature to assume that all specimens that have been assigned to *L. serratipalpe* in the past are examples of *L. euserratipalpe*. It is possible, for example, that subadult males of *L. calcar* or individuals with reduced retrorolateral femoral apophyses on the palp have indeed been misidentified as this species. A more thorough examination of the harvestman fauna of the Appalachian Mountains and points north and west is needed to firmly establish the geographic range of *L. euserratipalpe*.

Leiobunum calcar (Wood 1868)
(Figs. 33–46)

Phalangium calcar Wood 1868:26–27, fig. 6.

Liobunum calcar (Wood): Weed 1887:935; Weed 1889a:90–91; Weed 1889b:102–103; Weed 1890:918; Weed 1893a: 553–554; Weed 1893b:290–291; Banks 1893:211; Banks 1894:page?; Banks 1901:675; Roewer 1910:219; Roewer 1923:899, fig. 1054; Walker 1928:163, pl. 1, fig. 9.

Liobunum brunnea Walker 1928:167, pl. 2, fig. 12 (synonymized by Davis 1934:670).

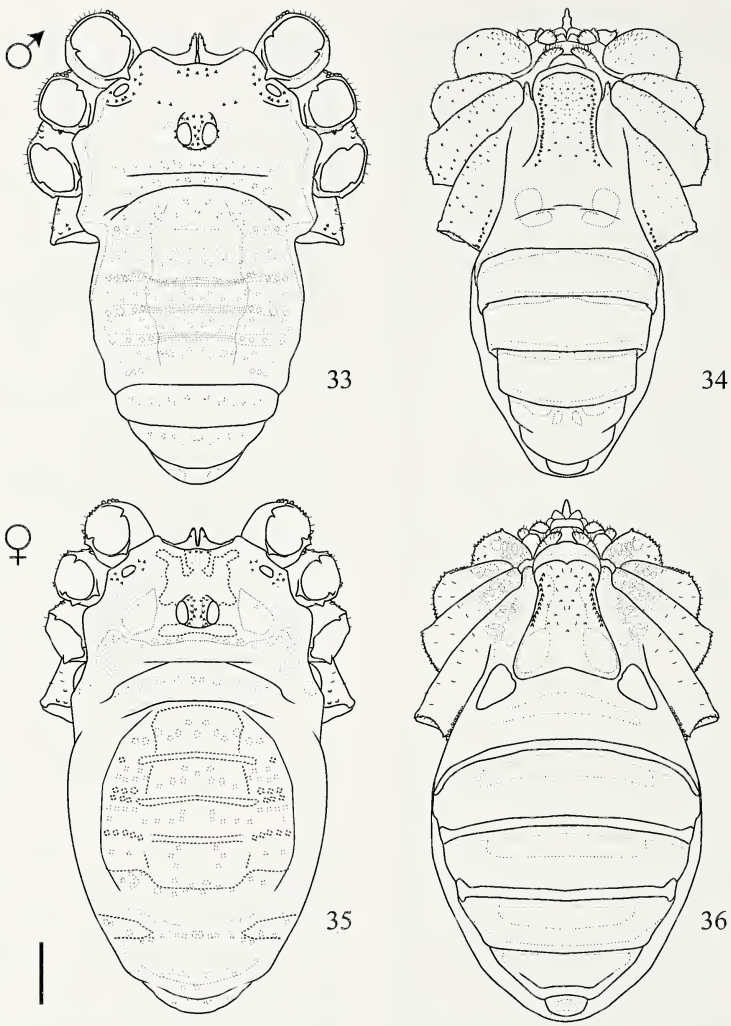
Leiobunum calcar (Wood): Crosby 1904:256; Davis 1934:670–672, pl. 32, figs. 16, 17, pl. 33, fig. 31; Bishop 1949:189–190, pl. 3, figs. 43–50; Edgar 1966:360, fig. 5; McGhee 1970:131–138, figs. 22a, 23b, 25a,b, 30, 31 [unpublished dissertation].

Leiobunum serratipalpe Roewer 1910:218; Roewer 1923:899, fig. 1054 (synonymized by Cokendolpher 1981:112–113).

"Leiobunum cumberlandense" McGhee 1970:122–128, figs. 21e, 23c, 24e, f, 30, 31 [unpublished dissertation]. NEW SYNONYMY.

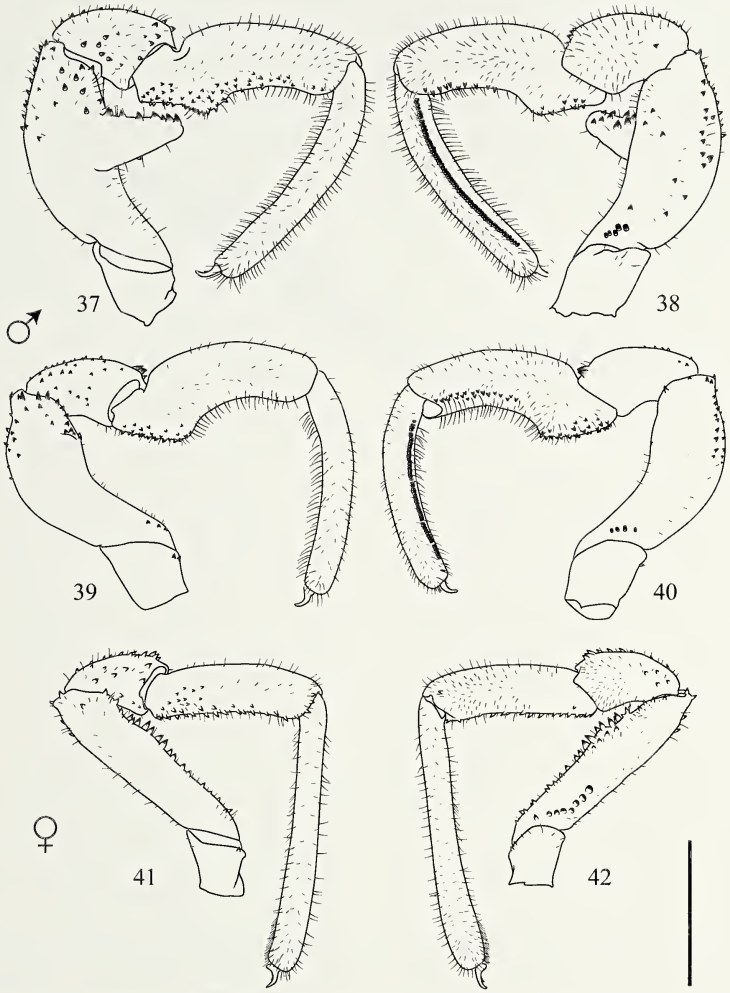
Type material.—*Phalangium calcar* Wood 1868. ♂ holotype, Type locality: "mountains of South-western Virginia". Not observed; presumed to be lost (Davis 1934:662).

Other material examined.—CANADA: *Ontario*: Manitoulin County: 1 ♂, Manitoulin Island, Square Bay, 45.75°N, 82.5°W, 26 July 1948, W. Ivie (AMNH). Parry Sound County: 1 ♂, Osawa Island, Georgian Bay, 9 mi [14.5 km] SSW of Pointe au Baril, on rock, 45.27.548°N, 80.25.808°W, 3 July 2007, P. Miller, G. Stratton, B. Suter (UMD). Simco County: 1 ♀, Orillia, 44.68°N, 79.31°W, 27 July 1938, C.H. Curran (AMNH); 1 ♂, South of Stirling, 44.15°N, 77.39°W, 16 July 1965, J. & W. Ivie (AMNH). USA: *Illinois*: McLean County: 1 ♀, Bloomington, 40.4842°N, 88.9937°W, [?] June [?], coll.? (INHS: 0007); 1 ♀, Lawnridge, 40.644°N, 89.605°W, 26 October 1959, Butler (MCZ: 36720). *Iowa*: Dickinson County: 2 ♂, Okoboji, sweeping grass, 43.3876°N, 95.138°W, 13 July 1916, coll.? (NMNH); 4 ♂, 7 ♀, same locality, [?] 1918, TCS (NMNH). *Kentucky*: Bell County: 1 ♀, Pine Mt. State Park, 36.7448°N, 83.7195°W, 27 August 1965, A. & L. Davis (AMNH: "*L. cumberlandense*"), 2 ♂, same locality, 2 August 1963, A. & L. Davis (AMNH: "*L. cumberlandense*"); 1 ♂, same locality, 23 August 1966, A. & N. Davis (AMNH: "*L.



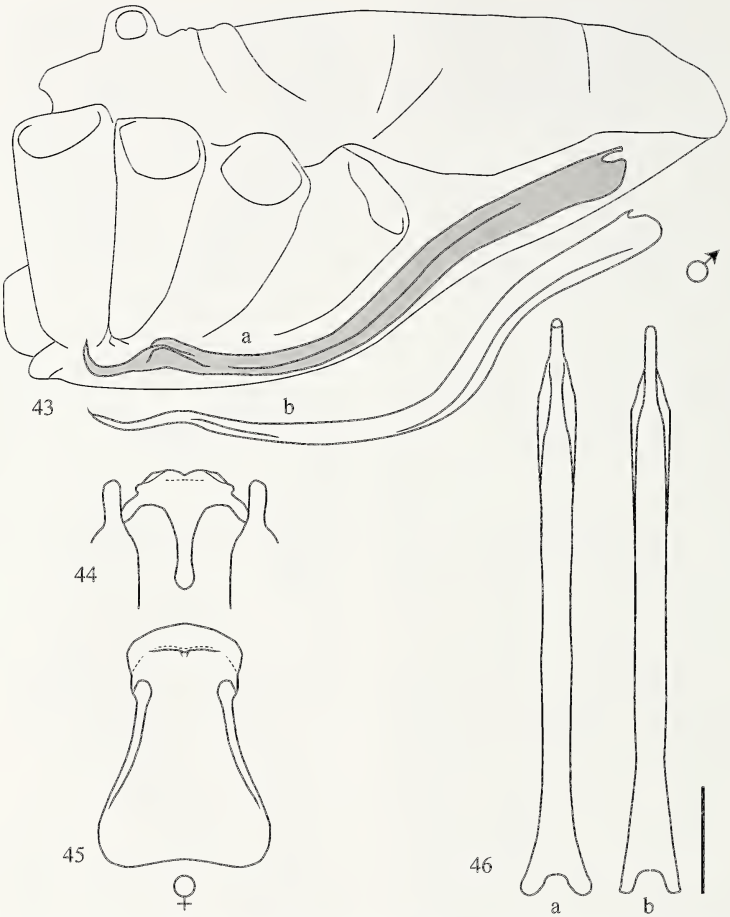
Figures 33–36.—Dorsal and ventral perspectives of *Leiobunum calcar* (Wood 1868), typical male and female from type region. Scale bar = 1 mm.

cumberlandense"). Knox County: 1 ♂, 1 ♀, Wooded hillside Trace Branch, near Heidrick, 36.8935°N, 83.8596°W, 17 June 1962, A. Davis (AMNH). Laurel County: 2 ♂, 1 ♀, Cumberland Natl. Forest [as of 1966, Daniel Boone National Forest], 36.8558°N, 84.3474°W, 22 August 1965, L. Davis (AMNH: "*L. cumberlandense*"). *Maine*: Washington County: 3 ♂, 3 ♀, 8 km S. Milbridge, 44.4619°N, 67.8929°W, 22–27 July 1990, coll.? (AMNH). Penobscot County: 1 ♂, 1 ♀, Howland, 45.2387°N, 68.6636°W, 5 July 1987, coll.? (TTU-Z 58,786). *Maryland*: Garrett County: 2 ♂, 2 ♀, 3 km SE New Germany, "Managed Oak Forest," (132, lot 003), 39.62°N, 79.105°N, elev. 779 m, 11–18 July 2005, M. Sarver (UMD). *Massachusetts*: Berkshire County: 13 ♂, 5 ♀ Lenox W. Mtn. Rd., Pleasant Valley Wildlife Sanctuary, 42.3513°N, 73.3378°W, [?] July 1976, J. Coddington (NMNH). *Michigan*: Charlevoix County: 1 ♂, no specific locality (county center used for coordinates), 45.318°N, 85.2584°W, T.H. Hubbell (AMNH). Cheboygen County: 2 ♂, 2 ♀, no specific locality (county center used for coordinates), 45.48°N, 84.50°W, 7 July 1983, coll.? (TTU Z-58,833); 1 ♂, Douglas Lake, Hook Point, 45.5674°N,



Figures 37–42.—Palps of *Leiobunum calcar* (Wood 1868): 37, 38. Typical male from type region, southwestern Virginia; 39, 40. Male "*cumberlandense*" variant; 41, 42. Typical female from type region. Retrolateral perspectives on left, prolateral perspectives on right. Scale bar = 1 mm.

84.6797°W, 3 July 1931, E.L. Miner (AMNH). St. Claire County: 3 ♀, New Baltimore, 42.6811°N, 82.7369°W, 5 July 1944, B. Malkin (AMNH). *Missouri*: Lincoln County: 2 ♂, 2 ♀, Cuivre River State Park, Hamilton Hollow Trail, elev. 550 ft [168 m], 39.03°N, 90.93°W, 21 June 1986, N.V. Horner (TTU Z-58,799). *New York*: Albany County: 5 ♂, Rensselaerville, 42.4794°N, 74.172°W, 15 July 1975, T. Eisner (AMNH). Chautaugua County: 2 ♀, Chautaugua, 42.2098°N, 79.4667°W, July–August 1943, C. Widmer (AMNH). Herkimer County: 1 ♂, 1 ♀, Little Falls, 43.0434°N, 74.8596°W, 3 July 1918, coll.? (AMNH). Madison County: 1 ♀, Deruyter Lake, 42.8145°N, 75.8978°W, 3 July 1922, coll.? (AMNH). Oneida County: 1 ♂, Trenton Falls, 42.2715°N, 75.1602°W, 5 June 1931, coll.? (AMNH). Tioga County: 1 ♀, Spencer, 42.2124°N, 76.4963°W, 5 August 1923, coll.? (AMNH). Tompkins County: 4 ♂, 1 ♀, Ellis Hollow, 42.4273°N, 76.4108°W, 28 July 1932, N.W. Davis (AMNH); 1 ♂, Freeville, 42.514°N, 76.3466°W, 10 August 1924, Swank (AMNH). Uister Co: 1 ♂, Cherrytown near Kerhonkson, 41.8251°N, 74.3293°W, 18 July 1976, Wygodzinsky (AMNH). *North Carolina*: Jackson County: 1 ♀, Whitewater Falls, Parking



Figures 43–46.—Genital structures of *Leiobunum calcar* (Wood 1868): 43. Diagrammatic lateral perspective of male showing position of penis; a. typical male, b. "*cumberlandense*" variant (southwestern Kentucky); 44. Ventral perspective of female sternum (genital operculum removed); 45. Dorsal (internal) perspective of female genital operculum; 46. Dorsal perspective of penis; a. typical male, b. "*cumberlandense*" variant (southwestern Kentucky). All to same scale. Scale bar = 1 mm.

Area, 35.071°N, 82.887°W, 28 August 1973, R.M. Shelley (NCMNS: 1937); 1 ♂, Brushy Fork of Greens Creek, 35.3249°N, 83.2822°W, 27 July 1971, F. Coyle (TTU Z-58,831); 1 ♂, Richland Balsam Mountain, elev. 6300–6400 ft [1920–1950 m], 35.3673°N, 82.9904°W, 4 August 1970, F. Coyle (TTU Z-58,783); 1 ♀, Dulany Bog at SR 1100 × 108 S of Cashiers, elev. 3020 ft [940 m], 35.0306°N, 83.0656°W, 21 July 1975, F. Coyle (TTU-Z 58,786). Cherokee County: 1 ♂, 11.2 mi [18 km] NW Murphy, along 1326, 35.222°N, 84.160°W, 27 July 1974, R.M. Shelley (NCMNS: 2437). Macon County: 1 ♂ 1 ♀, 5 mi [8 km] N of Highlands, 35.1269°N, 83.1924°W, August 1967, K. Kleinpeter (AMNH), 2 ♂, same locality, 9 July 1958, Hoffman (NMNH); 1 ♀, Highlands, "at Kleinpeter's place," 35.0365°N, 83.1921°W, 22 July 1967, Hoffman & Kleinpeter (VMNH), 2 ♂,1 ♀, Coweeta Hydrologic Station, 35.0596°N, 83.4205°W, 22 July 1977, L. Reynolds (NCMNS: A6823), 2 ♀, same locality, 22 September 1977, L. Reynolds (NCMNS: A6812, A6864), 1 ♀, same locality, 11 August 1978, L. Reynolds (NCMNS: A5258), 1 ♀, same locality, 6 September 1977, Lee Reynolds (NCMNS: A6818); 1 ♀, Glen Falls, 2 mi [3.2 km] SW Highlands, 3200 ft [975 m], 35.031°N, 83.238°W, 18 July 1988, K. Smith (NMNH); 1 ♂, Highlands Biological Station, elev. 3840 ft [1170 m], 35.054°N, 83.189°W, 18–28 July 1988, A.W. (NMNH); 1 ♂, Satulah Mtn., 1 mi [1.6 km] S of Highlands, 4500 ft [1372 m],

35.036N, 83.192W, 19 July 1988, W.A. Shear (VMNH). McDowell County: 1 ♂, Curtis Creek Campground, FR 482 N of Old Fort, 35.6889°N, 82.1976°W, elev. ~560 m, 20–21 August 2007, M. Hedin et al. (UMD). Swain County: 1 ♀, GSMNP, Clingman's Dome area, spruce-fir forest, 6500 ft [1981 m], 35.5627°N, 83.4985°W, 26 July 1988, AWS (NMNH). Transylvania County: 1 ♂, Davidson River Campground, off Hwy. 276, elev. ~650 m, 35.2813N, 82.7234W, 19–20 August 2007, M. Hedin (UMD); 1 ♂, 6.6 mi [10.6 km] WNW Brevard, Gov. Rd., 3.5 mi W Fish Hatchery, 35.26°N, 82.85°W, 29 August 1973, R.M. Shelley (NCMNS: 1992). Yancey County: 1 ♂, Mt. Mitchell, "camping area near top", 35.7601°N, 82.2709°W, 31 July 1972, R.L. Hoffman (VMNH). *Ohio*: Ottawa County: 1 ♂, Catawba Island, 41.583°N, 82.8346°W, date?, J.S. Hine (NMNH). *Pennsylvania*: Columbia County: 6 ♂, 1 ♀, Orangeville, 41.339°N, 80.519°W, 13 August 1932, Hughes & Davis (AMNH). Erie County: 1 ♀, no specific locality [counter center used for coordinates], 42.10°N, 80.10°W, 24 June 1987, C. Tugman (TTU-Z 58,708). *Tennessee*: Blount County: 3 ♂, Cades Cove, GSMNP, 35.4950°N, 84.0227°W, 12 September 1959, coll.? (AMNH). Cocke County: 1 ♂, Albright Grove, "ATBI Plot," 35.9359°N, 83.1220°W, 19 June–6 July 2001. M. McCord (NPS); 2 ♂, GSMNP, vic. Cosby ATBI residence house, 35.7779°N, 83.2135°W, elev. 518 m, 28 July–9 August 2000, M. Hedin, J. Cokendolpher (AMNH). Sevier County: 1 ♂, GSMNP, trail up Mt. Leconte, 35.6542°N, 83.4372°W, September 1959, PC Holt (NMNH); 1 ♂, 2 ♀, GRSM ATBI Plot: Goshen Prong, 35.6105°N, 83.5453°W, 27 August–17 September 2001, I.C. Stocks (NPS); 1 ♂ 2 ♀, Great Smoky Mtns., ATBI Plot: Indian Gap, 35.6108°N, 83.4436°W, 6 August–3 September 2001, R. Fox (NPS), 1♂, same locality, 35.6108°N, 83.4436°W, 3–26 September 2001, I.C. Stocks (NPS); 1 ♂, 1 ♀, Great Smoky Mtns., ATBI Plot: Twin Creeks, 35.685°N, 83.499°W, 10–30 September 2002, coll.? (NPS), 1 ♂, 1 ♀, same locality,5–18 July 2000, Parker, Stocks, Petersen (NPS), 1 ♀, same locality, 26 September–12 October 2000, Parker, Stocks, Petersen (NPS), 1 ♀, same locality, 15–23 May 2001, I. Stocks, M. Williams (AMNH). Pickett County: 3 ♂, 3 ♀, Pickett State Park, 36.558°N, 84.7916°W, 25 June 1967, C.R. McGhee (AMNH: "*L. cumberlandense*"). Roane County: 3 ♂, Kingston, 35.8809°N, 84.5085°W, 12 July 1933, W.J. Gertsch (AMNH). *Vermont*: 3 ♀, North Danville, 44.459°N, 72.094°W, 13 August 1967, A.M. Chickering (MCZ: 37203). 1 ♀, Lake Bomoseen, 43.645°N, 73.225°W, 10 July 1936, coll.? (MCZ: 37147). *Virginia*: Amherst County: 4 ♂, 1 ♀, Tarjacket Ridge, 37.4316°N, 78.6569°W, 9 July 1998, J. Schilling (VMNH); 3 ♂, 1 ♀, same locality, 4 August 1998, VMNH survey (VMNH). Augusta County: 1 ♂, GWNF, 5 mi [8 km] west of Stokesville Comp., "452-8A Trap 3," 38.3403°N, 79.2334°W, 8 July 1989, B. Flamm (VMNH); 1 ♂, GWNF, ca 5 mi [8 km] west of Stokesville Comp., "460-3 Trap 3," 38.3403°N, 79.2334°W, 1 September 1989, B. Flamm (VMNH). Bath County: 2 ♂, SE of Hot Springs, "crest of Warm Springs Mtn.," 38.0526°N, 79.7684°W, 19 August 1999, S.M. Roble (VMNH); 1 ♂, "headwaters of Smith Creek, across Middle Mtn. from Douthat State Park," 38.5713°N, 78.8298°W, 9 July 1988, R.L. Hoffman (VMNH); 2 ♂, Warm Springs Mtn, WFD, UV, 38.0526°N, 79.7684°W, 14 June 1999, J.C. Ludwig (VMNH). Botetourt County: 1 ♂, 3 ♀, Roaring Run, 37.6924°N, 79.8909°W, 21 August 1996, M. Donahue (VMNH). Clarke County: 1 ♂, 1 ♀, Blandy Farm, ca 3 mi [4.8 km] south of Boyce, 39.0624°N, 78.0622°W, 2 July 1991, D.R. Smith (VMNH); 5 ♀, same locality, 1 August 1991, D.R. Smith (VMNH). Dickenson County: 1 ♀, Breaks Interstate Park, "DF site 2, Nature Trail," 37.287°N, 82.296°W, 22 August–6 October 1991, VMNH survey (VMNH). Essex County: 3 ♂, 1 ♀, 1.5 km SE Dunnsville, "Malaise trap B1#1," 37.8473°N, 76.8015°W, 12 July 1991, D.R. Smith (VMNH). Floyd County: 1 ♂, Buffalo Mountain NAP, "north slope DF site," 36.796°N, 80.477°W, 15 July–29 August 2001, VMNH survey (VMNH); 3♂, 1 ♀, Buffalo Mountain NAP, "south slope DF," 37.4316°N, 78.6569°W, 9 August–6 September 2000, Joint Survey (VMNH). 1 ♀, Buffalo Mountain NAP, "UV trap at base of hump," 37.4316°N, 78.6569°W, elev. 1067 m, 3 June 2000, S.M. Roble (VMNH); 1 ♂, 1 ♀, Buffalo Mountain NAP, "trailhead at parking lot," 37.4316°N, 78.6569°W, 2 June 2004, R.L. Hoffman (VMNH); 2 ♀, Buffalo Mountain NAP, "upper foot trail to top," 37.4316°N, 78.6569°W, 29 July 2000, Joint Survey (VMNH); 4 ♂, Buffalo Mountain, ~1300 m, 6 mi [9.7 km] SE of Willis, 36.796°N, 80.477°W, 25 August 1984, R.L. Hoffman (VMNH). Giles County: 1 ♀, Mountain Lake, 37.3551°N, 80.5368°W, June–July 1947, H.H. Hobbs, Jr. and Zoology class (TTU); 1 ♂, Mountain Lake, 3800 ft [1158 m], 37.3551°N, 80.5368°W, [?] June 1959, Holt & Hoffman (NMNH). Henry County: 1 ♂, Breeski's Farm, "near Ridgeway," 36.9893°N, 79.4825°W, 22 August 1987, VMNH Exped (VMNH). Highland County: 1 ♂, Locust Springs, "Buck Run ponds," 38.5828°N, 79.6352°W, 5 August 1999, S.M. Roble (VMNH); 1 ♂, Locust Spring Recreation Area, 8 mi [13 km] NW of Bluegrass, 38.5828°N, 79.6352°W, elev. 1158 m, 13 July 1974, R.L. Hoffman (VMNH). Lee County: 1 ♂, Cumberland Gap National Historical Park, 36.623°N, 83.645°W, 13 June 1965, N. Davis (AMNH: "*L. cumberlandense*"). Montgomery County: 3 ♂, Blacksburg, 37.2296°N, 80.4139°W, 15 July 1956, Hoffman (NMNH). Nelson County: 2 ♂, The Priest, 4.5 mi [7.2 km] SE of Montebello, 37.8199°N, 79.0625°W, elev. 1189 m, 16–29 August 1991, VMNH survey (VMNH); 1 ♂, The Priest, "at drift fence site," 37.8199°N, 79.0625°W, elev. 1189 m, 20 September 1991, R.L. Hoffman (VMNH); 2 ♂, North Fork, Tye River, ~4 mi [~6.5 km] E of Montebello on Va. 687, PF, 37.8595°N, 79.0446°W, 6 September 1998, VMNH survey (VMNH). Russell County: 1 ♂, Cedar Creek Falls, ca 4 mi [6.4 km] NE of Lebanon, 36.9542°N, 82.0541°W, 2 July 1989, R.B. & R.L. Hoffman (VMNH). Wise County: 1 ♂, 0.8 mi [1.3 km] NW of Tacoma on VA Hwy.706, mixed woods, dry hillside, 36.9408°N, 82.5448°W, 19 July 1989, R.L. Hoffman (VMNH).

Diagnosis.—Penis (Figs. 43a, b, 46a, b): shaft with broad ventral bend in lateral view, followed by smaller dorsal bend subterminally in region of alae; alae varying from large and dorsally curved to essentially absent; glans curved dorsally. Male retrolateral apophysis present on palpal femur, varying from large (Fig. 37) to scarcely developed (Fig. 39) but always associated with a field of stout, pointed denticles. Female palpal femur usually with low retrolateral apophysis covered in enlarged spine-like denticles (Fig. 41). Posterior margin of female sternum with long median process (greater than half sternum width) projecting into soft cuticle of pregenital chamber, process essentially doubling length of sternum; anterior sternal margin usually with narrow median notch (Fig. 44), sometimes apparently absent.

Description of typical male from type region (Virginia: Buffalo Mountain NAP, "trailhead at parking lot," 37.4316°N,

78.6569°W, 20 June 2004, R.L. Hoffman (VMNH).—Body length: 6.5 mm. *Dorsum* (Fig. 33): Carapace length, width: 2.0 mm, 3.4 mm. Surface granulate and light brown to golden yellow-brown with medium brown bordering extending from the lateral margin of carapace to anterior opisthosoma margin. Anterior median prominence with 1 median denticle and a row of 2–3 lateral denticles on each side. Mesopeltidium and metapeltidium distinct medially, merging laterally; each with a single row of white dots; posterior margins light brown and rebordered. Ocularium reddish-brown with a dark circumocular band and acanaliculate, with a loose circle of 15 sharp, dark-tipped denticles and a few interspersed short erect setae around each eye; anterior denticles point posteriorly, posterior denticles point anteriorly, dorsal denticles larger and more numerous. Ozopore mound with sharp denticles scattered on all but the anterior-lateral surface, with a few extending to the ocularium. Supracheliceral lamina arching ventromedially with parallel parts divided by a deep cleft; sharp, distally-pointing dark-tipped denticles on dorsal and anterior surfaces. Opisthosoma: Tapers posteriorly; surface granular with a few tiny scattered setae laterally; predominantly light brown with a very faint central figure beginning around the ocularium and fading at tergite 6. Rows of sigilla demarcate tergites 1–6 lateral to central figure; tergites 1–7 with a complete medial transverse band of white spots and whitish anterior and posterior bordering; tergite 8 with two large lateral posterior sigilla. Anal operculum light brown with medial white blotch and a few scattered setae and small sharp denticles. *Venter* (Fig. 34): Labrum curved dorsally with a rough ventral surface. Sternites light yellow with white bordering on posterior margin and light brown on anterior margin; sparse erect setae scattered over surface. Sternite 3 overlaps sternite 4, sternite 4 overlaps sternite 5; sternites 7 and 8 fused medially but distinct laterally; posterior margin of sternites 3 and 4 slightly recurved, all other margins straight. Genital operculum yellowish and somewhat transparent posterior-medially; anterior margin strongly rebordered and whitish with a dark medial blotch; submarginal row of small, sharp, dark denticles lateral, smaller rounded denticles and setae scattered on medial surface. Genital operculum and sternites 2 and 3 fused; the posterior operculum margin demarcated by a shallow, incomplete recurved crease. Large sigilla on posterior lateral surface of operculum extend to anterior portion of sternite 3. Sternum simple, slightly narrower medially.

Appendages: *Chelicerae*: Light golden brown with slightly darker dorsal surface on proximal article, small dark retrodorsal blotches on distal article; setae scattered on dorsal surface of both articles, becoming denser distally and forming a distal prolateral row on distal article and a submarginal row on proximal article.

Palps (Figs. 37, 38)*:* Measurements in mm: femur 1.7; patella 0.8; tibia 1.5; tarsus 1.7. Trochanter light golden brown with distal prolateral row of erect setae. Femur brown, darker distally; narrow basally (but proximal dorsal surface slightly inflated), becoming strongly inflated and arched distodorsally, then narrowing slightly at distal end; ventral surface slightly curved. Sharp denticles and setae scattered on distal prolateral and dorsal surfaces and arranged in a dorsal retrolaterally curving row and a proximal prolateral row of 4 large denticles on the left femur, 6 on the right. Distal retroventral surface with a large (0.6 mm) conical "spur" or apophysis projecting ventrolaterally. A dense field of sharp denticles and interspersed setae extends from anterior apophysis surface to distal femoral margin. Patella dark brown; dorsal surface 3–4 times the length of the ventral surface; distal prolateral surface slightly protuberant; an irregular row of dark distally pointing denticles extends along the dorsal to retrolateral margin; smaller denticles scattered retrolaterally and in loose dorsal row; scattered erect setae cover all but the ventral surface. Tibia golden brown with darker dorsal and retrolateral blotches. Proximal dorsal surface slightly inflated; proximal ventral surface expanded, forming a large flat prominence densely covered with proximally-pointing, sharp, dark denticles. Ventral surface arched distal to prominence and covered with long erect setae. Dark denticles form a proventral band and loose distal retroventral row. All but the retrodorsal surface with a coat of dark, erect setae. Tarsus light golden brown and curving slightly ventrally and retrolaterally; tightly-packed proventral row of dark, flat-topped denticles extend nearly the full length of the tarsus; 6–7 rows of dark erect setae covering all but the ventral surface; short recumbent setae cover the surface, and fine erect setae form a scopula-like structure distoventrally. Tarsal claw golden brown with a dark tip with 6 teeth.

Legs: Measurements of femur, patella, tibia, metatarsus, tarsus in mm: I: 5.7, 1.6, 5.4, 6.1, 7.0; II: 11.0, 1.8, 10.7, 10.8, 22.4; III: 5.5, 1.5, 4.9, 7.1, 9.6; IV: 8.1, 1.8, 7.1, 11.8, 13.5. Coxae yellowish with condyles and proximal posterior margin dark; short erect setae and tiny blunt denticles scattered over surface and forming a ventral submarginal row. Coxae I and II with an anterior row of flat-topped denticles, coxa IV with a posterior row of flat-topped denticles. A few small denticles scattered on anterior surfaces of coxa III and IV, posterior of III, but not forming a distinct row. Coxa II with large dark-tipped denticle on posterior margin. Trochanters dark brown; small, distally pointing denticles scattered on dorsal, prolateral, and retrolateral surfaces and arranged in a distal submarginal circumferential row; dorsal surface with distal medial longitudinal groove. Femur base dark brown, wider proximally, with scattered distally-pointing denticles on pro- and retrolateral surfaces; distinguished from shaft by a circumferential groove; shaft light golden brown, dark brown distally (except femur II); distally-pointing dark-tipped denticles and accompanying distally adjacent seta arranged in 5–7 irregular longitudinal rows, more defined dorsally, absent ventrally (femur I denticles denser, rows less defined); distal ventral margin with a row of dark-tipped denticles, distal dorsal margin with 2 distally pointing denticles. Patellae with 4–6 loose longitudinal rows of tiny denticles and a distal submarginal row of larger denticles, cuticle dark brown. Tibiae golden brown, darker distally (except tibia II); tiny distally-pointing denticles arranged in 5–8 proximal longitudinal rows; each denticle accompanied by a distal erect seta, with setae continuing each row distally; tibia II with setae rows only and a few tiny denticles; distal margin with a ventral row of small denticles terminating in a single spine at either end (tibia II with spines only); surface with a coat of recumbent setae; vestiture of microtrichia present, especially distally. Tibia II with 5 incomplete pseudoarticulations. Metatarsi with 6–8 pseudoarticulations, each with a pair of distally pointing

ventral spines and a dark dorsal blotch; 5–6 rows of erect setae extend down the metatarsus and tarsus; metatarsi and tarsi golden brown with a coat of recumbent setae. Tarsi with fine, dense, erect setae on ventral surface, denser distally; longer (proximal) telotarsi with 2 distally pointing ventral spines on distal margin. Claw smooth.

Penis (Figs. 43a, 45a): 5.1 mm long. Dorsoventrally flattened (rounder basally), with a lateral ridge down most of the length of both sides of the shaft; base expanded laterally at attachment to stabilizing rods; shaft curved dorsally, thickly sclerotized distally. Alae thick and angled dorsally, with shaft bulging dorso-medially between alae; glans curving 90° dorsally and stylus projecting dorsally from tip.

Variation in male.—The species displays substantial variation in several characters. The central figure and dorsal rows of white spots and darker markings vary from apparent to faded, or may be absent. Trochanters and basal portions of the femora are generally dark, often contrasting with the femoral shaft but are concolorous. The legs and palps range from golden to dark brown. Denticle density varies on the carapace, particularly between the ozopore mound and median prominence, as well as on the coxa, although the presence or absence of rows shows little variation. The fusion between the genital operculum and sternites 2 and 3 may be partial or complete. The palps may occasionally be less robust, but not slender, and have a reduced but still-evident retrolateral apophysis (Figs. 39, 40). Penis curvature varies from shallow to pronounced, and alae may be horizontal (Figs. 43b, 46b) rather than angled dorsally, or reduced to a thickly sclerotized region near the base of the glans.

Description of typical female from type region: U.S.A.: Virginia: Floyd County: Buffalo Mountain NAP, "trailhead at parking lot," 37.4316°N, 78.6569°W, 20 June 2004, R.L. Hoffman (VMNH).—Body length: 7.5 mm. *Dorsum* (Fig. 35): Carapace length, width: 2.0 mm, 3.3 mm. Supracheliceral lamina similar to that of the male. Ozopore mound with a few scattered sharp denticles laterally. Ocularium acanaliculate but appearing canaliculate due to a dark medial band and lighter circumocular band; each carina with 10 sharp dark denticles; anterior denticles larger and point posterior, posterior denticles smaller and point anterior. Anteromedian preocular prominence light brown with two brown longitudinal stripes and a submarginal row of 4 small denticles. Cuticle between ocularium and median prominence dark brown with a dense field of tiny dark rounded tubercles, giving a coarsely granulate texture. Anterior margin of mesopeltidium slightly elevated above surface of propeltidium and fading laterally into the carapace surface; cuticle brown with white lateral blotches and medial anterior margin that breaks up to white dots laterally; posterior and lateral margin dark brown. Metapeltidium medium brown, white laterally, with posterior and lateral dark brown bordering and an anterior row of white dots. Opisthosoma: Rounded and gently tapering posterior. Tergites 1–5 marked by a slight ridge halfway between the medial and lateral lines of the dorsum, creating a distinct rounded medial region; cuticle coarsely granular with tiny rounded tubercles less dense but more distinct lateral (distal) to the ridge. Central figure defined by medium-dark bordering extending from tergite 1 to the anterior margin of tergite 5 and continuing as 2 dark anterior blotches on remaining tergites. Tergites 1–4 medium to dark brown, lighter laterally (distal to ridge), medial region with transverse rows of white dots along each tergite and short rows of small dark brown dots separating tergites between central figure and ridge. Remaining tergites light to golden brown, darker laterally, with medial white dots. Anal operculum medium brown with large white medial blotch and a few small submarginal denticles.

Venter (Fig. 36): Sternites 3–6 smooth, light brown, anterior and posterior margins fading to white, with a brown anterior border; sternite 7 + 8 white with light brown posterior bordering and 4 medium brown dots in 2 rows; posterior and lateral margins rebordered. Genital operculum, and all sternites distinct. Operculum white medially and golden brown laterally with 2 large posterior sigilla; two smaller sigilla extend from proximal half of sternite 2 to anterior margin of sternite 3. Setae and small denticles scattered medially on operculum, sharp, dark-tipped denticles arranged in a lateral submarginal row; anterior denticles larger and denser. Anterior margin thickly rebordered and protruding, forming a whitish "lip" and a transverse sulcus with a corresponding transverse phragma on the inner (dorsal) surface; anterior body of operculum protuberant and slightly bilobed just posterior to transverse sulcus, forming a short medial sulcus and corresponding inner medial ridge in the posterior space formed by the phragma (Fig. 45). Sternum anterior margin notched medially and slightly angled ventrally; median posterior process as long as sternum width (Fig. 44). Labrum straight and expanded ventrally at base.

Appendages: *Chelicerae*: Light golden brown. Proximal article with medium brown dorsal surface and distal submarginal row of setae, second article with small dark retrodorsal blotches and setae scattered on dorsal surface and arranged in imperfect pro- and retrolateral rows (denser and less organized distally).

Palps (Figs. 41, 42): Measurements in mm: femur 1.6; patella 0.7; tibia 1.2; tarsus 1.9. Trochanters golden brown with a distal retroventral row of setae and small median submarginal tubercle. Femur medium brown, darker dorsally; diameter slightly increases distally. A low, rounded process and a few large dark denticles located at the retrolateral position corresponding to the more prominent male apophysis. Parallel pro- and retroventral rows of denticles diverge distally, retroventral row terminating in short submarginal retrolateral row of smaller denticles; a few distally-pointing denticles scattered on distodorsal surface and arranged in a prolateral submarginal row; erect setae interspersed with denticles and forming a prolateral row; 8 large denticles form proximal prolateral row, with proximal half abruptly curving ventrally. Patella medium brown, dorsal surface twice the length of the ventral surface and wider distally; prolateral margin slightly protuberant. Erect setae cover all but the retroventral surface; distally pointing denticles form 2 dorsal rows and a loose retrolateral row, with a few small denticles scattered distal-retroventrally and proximal-prolaterally. Tibia golden brown, darker dorsally, with a coat of short recumbent setae and a single distal prolateral denticle; a ventral row of dark-tipped, distally-pointing denticles terminates in a distal retrolateral submarginal row; proximal denticles denser, smaller and more scattered, becoming a small retrolateral field; erect setae arranged in a retrolateral row and scattered

on dorsal, ventral, and distal prolateral surfaces. Tarsus golden brown with a narrow proventral dark stripe corresponding to the male denticle row; dense recumbent setae and 6–8 rows of dark erect setae extend the length of the tarsus (denser distally) with dense, fine, erect setae distoventrally; claw golden brown with 5–6 teeth.

Legs: Measurements of femur, patella, tibia, metatarsus, tarsus in mm: I: 6.3, 1.7, 5.2, 6.9, 9.6; II: 11.4, 1.7, 10.6, 11.4, 28.5; III: 6.0, 1.5, 5.2, 7.6, 10.2; IV: 8.5, 1.7, 7.7, 11.8, 14.2. Coxae golden brown with proximal golden brown blotches surrounded by white; surface smooth with scattered short erect setae and a ventral submarginal row of a few small denticles and interspersed setae (fewer denticles and more setae on coxae II and III). Coxae I, II, and III with anterior (prolateral) row of flat-topped denticles and tiny posterior (retrolateral) scattered denticles; coxa IV with posterior row of flat-topped denticles and small scattered denticles anterior; anterior coxa IV and posterior coxa II each with a dorsal submarginal denticle. Trochanters dark brown with denticles scattered on pro- and retrolateral surfaces (less dense on trochanter IV) and forming a distal circumferential submarginal row. Femur base defined by a circumferential groove and dark brown coloring, with distally-pointing denticles and erect setae scattered laterally and a few ventrally; shaft slightly expanded distally and golden brown with dark brown distal condyles, a submarginal row of distally-pointing sharp, dark denticles, and approximately 5 irregular rows of distally-pointing, dark-tipped denticles (densest on femur I) with accompanying distal erect seta (ventral surface bare). Patellae light brown with whitish mottling, especially on patella III; narrow white bordering on distal margin of patella I; small distally-pointing dark-tipped denticles with distally adjacent seta scattered over surface, some forming rows (reduced on patella II); a few larger denticles form a distal submarginal row. Tibiae golden brown with a coat of short recumbent setae; 5 proximal rows of distally-pointing dark-tipped denticles extending no more than half the length of the tibiae (reduced on tibia I); erect setae distally adjacent to each denticle continue in rows the full length of the tibia; distal ventral submarginal row of a few small, dark, distally pointing denticles terminate with a single spine at either end; vestiture of microtrichia present distally; tibia II lacking nearly all denticles, but with setae and spines as on other tibiae and 4 faint incomplete pseudoarticulations. Metatarsi golden brown with a coat of recumbent setae; 3–4 pseudoarticulations (8–9 on metatarsus II) each with a dark dorsal spot and a pair of dark, distally-pointing ventral spines; 5 rows of fine erect setae extend from metatarsus to proximal half of tarsus; longer (proximal) telotarsi with a distal pair of small ventral spines; surface with a dense coat of recumbent setae and a ventral scopula-like structure of fine, erect setae; tarsal claw smooth with a ventral tooth-like protuberance at base.

Ovipositor: Typical; two spermathecae visible between rings 6 and 7.

Variation in female.—The dorsal surface, palps, and legs vary from golden brown to dark brown, or even, rarely, predominantly white. The ventral surface ranges from white to dark golden brown, but is always lighter than the dorsal cuticle. Central figure may be more or less distinct and may begin on the carapace or tergite 1. Trochanters and femur base are often darker than the femur shaft, but can be concolorous. The number of denticles on the ocularium varies from a few to more than 20. Coxal denticle rows vary from dense, distinct rows to few and scattered. Sternum notch may be very shallow and the posterior sternal process ranges, although longer is more common. As in *L. euserratipalpe*, the posterior process completes its sclerotization during the adult stage and early-season (June) adults may appear to lack the process, although it may be present as a poorly sclerotized band. The small retrolateral femoral apophysis of the palp is sometimes greatly reduced, especially in smaller specimens.

Distribution.—*Leiobunum calcar* ranges from Saskatchewan (Holmberg 1998) to Newfoundland (Hackman 1956) in Canada. The northern limit is not known, but *L. calcar* appears to extend farther north than other North American *Leiobunum* species. This widespread distribution continues into the northern United States from the northern plains and Great Lakes Region to the New England States, with large regions remaining to be sampled (Fig. 47). The species appears to be increasingly restricted to the Appalachian Mountains in more southern states, which may reflect historical sampling effort or, if accurate, a propensity for cooler climates.

Remarks.—Male *L. calcar* are typically recognized by a prominent retrolateral femoral apophysis on the palp and a long, ventrally curved penis with large alae, and this is by far the most widespread association of characters in the species. However, there are many regional or even local variants that differ in the size of the retrolateral femoral apophysis and penial alae. McGhee (1970) proposed the species *L. cumberlandense* based on the association of reduced femoral apophysis and reduced alae in specimens from the Cumberland Region of Kentucky, Virginia, and Tennessee. However, specimens with well-developed femoral apophyses also occur in this region and are otherwise identical to *L. cumberlandense*. In addition, we have found several widely scattered populations with the *L. cumberlandense* syndrome (e.g., Manitaulin Island in Lake Huron and far-western Maryland). These and other variants may be monophyletic and reproductively isolated from other populations of *L. calcar*, but we cannot at present find compelling morphological evidence for this. In contrast, the subterminal dorsal bend in the penis and the presence of a long posterior sternal process in the female appear to be essentially universal features of the species.

Leiobunum hoffmani new species
(Figs. 48–61)

"Leiobunum hoffmani": McGhee 1970:141–147, figs. 34, 35 [unpublished dissertation]

Type material examined.—Holotype male: USA: *Virginia*: Smythe County: Mt. Rogers NRA, 36.724°N, 81.4904°W, elev. 870 m, 10 August 2007, M. Hedin (NMNH). Paratype: 1 female: USA: *Virginia*: Grayson County: Whitetop Mountain, "just off FS 89," 36.6387°N, 81.6059°W, elev. ~1524 m, 25 June–11 July 1998, VMNH Survey (NMNH).

Other material examined.—USA: *North Carolina*: Alleghany County: 2 ♂, 5 ♀, Doughton Park CG, "on BRP, S of Sparta," 36.4290°N, 81.1539°W, elev. 1100 m, 11 August 2007, M. Hedin (UMD). Wilkes County: 8 ♂, 3 ♀, Doughton National Recreation Area, Blue Ridge Parkway, 36.4016°N, 81.1748°W, 30 July 1967, C.R. McGhee (AMNH). *Virginia*:

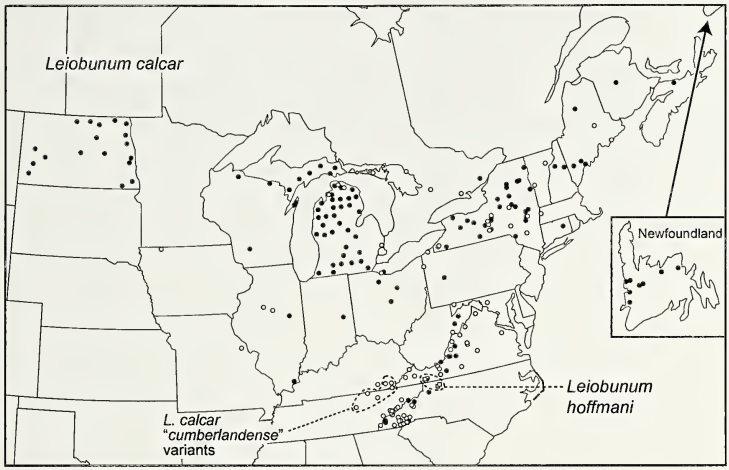


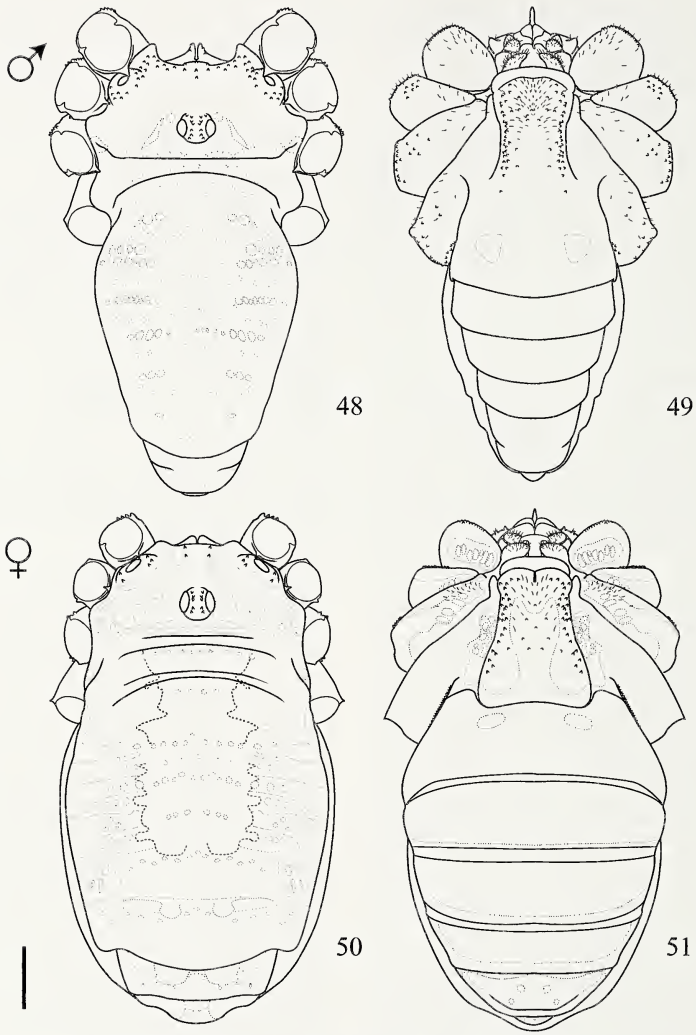
Figure 47.—Map of collection localites for *Leiobunum calcar* (Wood 1868) and *Leiobunum hoffmani* new species. Open circles are localities of *L. calcar* specimens observed in this study. Black circles are localities of *L. calcar* specimens obtained from the literature (Bishop 1949; Carter & Brown 1973; Davis 1934; Edgar 1971; Hackman 1956; Jennings et al. 1984; Katayama & Post 1974; Levi & Levi 1952; McGhee 1970; Weed 1889a). Open squares are localities of all known *L. hoffmani* specimens.

Grayson County: 12 ♂, 12 ♀, White Top Mountain, "just off FS 89," 36.6387°N, 81.6059°W, elev. ~1524 m, 25 June–11 July 1998, Virginia Natural History Survey (VMNH); 1 ♂, White Top Mountain, "beechwoods, off FS 89," 36.6387°N, 81.6059°W, elev. ~1524 m, 20 August 2001, Virginia Natural History Survey (VMNH), 6 ♂, same locality, 25 June–11 July 1993, Virginia Natural History Survey (VMNH); 3 ♂, 2 ♀ (penultimate), 1 ♂, 1 ♀ (antepenultimate), Grayson Highlands State Park, Haw Orchard Mountain, "above water tank," 36.6270°N, 81.5048°W, 2–15 June 1991, Virginia Natural History Survey (VMNH), 13 ♂, 3 ♀, same locality, 36.6270°N, 81.5048°W, 30 August 1990, Virginia Natural History Survey (VMNH), 3 ♂, same locality, 8 July 1990, R.L. Hoffman (VMNH); 1 ♂, 3 ♀, Mount Rogers, "horse trail to Helton Creek," elev. 1310–1370 m, 36.6599°N, 81.5451°W, 8 July 1990, R.L. Hoffman (VMNH); 10 ♂, 1 ♀, Highlands State Park, Haw Orchard Mountain, "spruce woods near Visitor Cntr," 36.6270°N, 81.5048°W, 8 August 1990, Virginia Natural History Survey (VMNH). 3 ♂, 1 ♀, Grayson Highlands State Park, E of Visitor Center & Pinnacles Trail on Haw Orchard Mtn., elev. ~1500 m, spruce forest with rock outcrops, 36.6247°N, 81.5013°W, 11 August 2007, M. Hedin (UMD). Smythe County: 5 ♂, 2 ♀, Mt. Rogers NRA, Hurricane CG, W of Hwy. 16, 36.7240°N, 81.4904°W, elev. 870 m, 10 August 2007, M. Hedin (UMD).

Etymology.—The species is named in honor of Richard L. Hoffman for his contributions to invertebrate taxonomy.

Diagnosis.—Penis (Figs. 58, 61) elongate (> 7 mm, full length of body or more) gradually tapered distally, alae absent. Male palp massive with terminally inflated, incrassate femur and proximally inflated, incrassate tibia; femur with large retrolateral apophysis lined distally with denticles (Doughton Park Region, North Carolina) (Fig. 52) or low naked protuberance (Grayson Highlands, Virginia) (Fig. 54), no known intermediates. Female sternum large with long posterior process and deep anterior median notch extending to middle of sternum (Fig. 59), palpal femur lacking the femoral apophysis (Fig. 56) of most female *L. calcar* (Fig. 41).

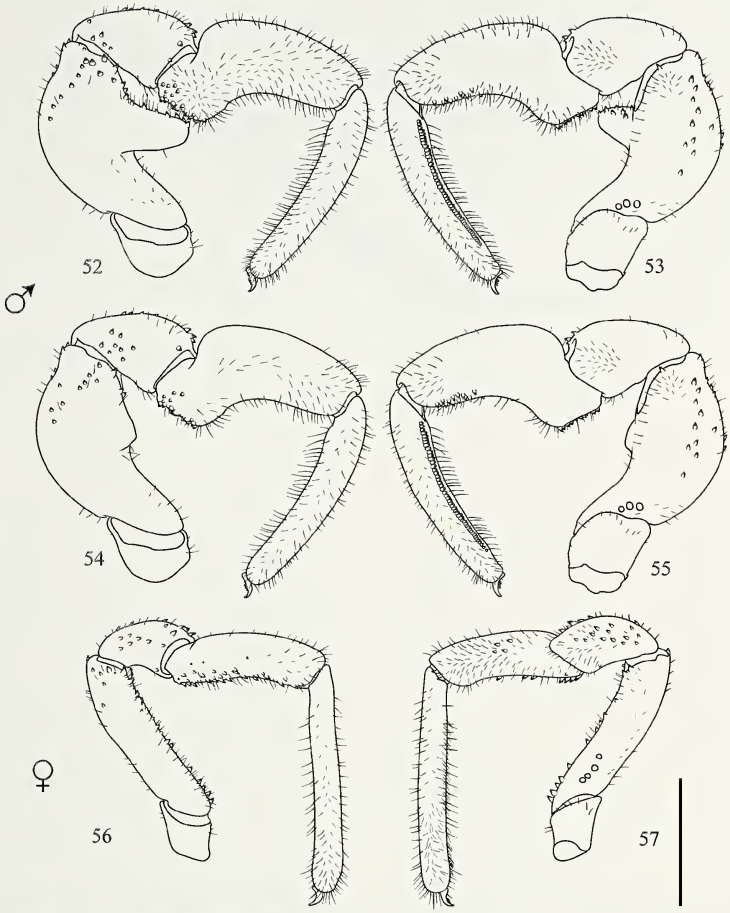
Description of male holotype.—Body length: 6.5 mm. *Dorsum* (Fig. 48): Carapace length, width: 1.8 mm, 3.5 mm. Supracheliceral lamina with a few small denticles on anterior and dorsal surfaces. Anterior median prominence with three loose longitudinal rows (one median, two lateral) of two or three small, sharp denticles; additional denticles scattered between prominence and ozopore, particularly along anterior carapace margin. Ozopore mound with sharp denticles at anterior and posterior ends, smooth with a few small setae laterally. Ocularium dark brown and weakly canaliculate; each carina with 10 sharp, curved denticles nearly circling the eye; anterior denticle pointing posterior, posterior denticles pointing anterior. Transverse postocular fold distinct medially, fading into general carapacal surface laterally; a transverse row of whitish dots extends across meso- and metapeltidium. Posterior margin recurved and rebordered. Cuticle otherwise orange-brown and granulate. Opisthosoma: Elongate, tapering posteriorly. In lateral view, dorsal surface bends gradually upward and then posteriorly. Granular cuticle predominantly light orange-brown and lacking a central figure. Scutal tergites (tergites 1–5) and free tergites 6 and 7 demarcated by lateral sigilla and a transverse band of white spots. A pair of large oval sigilla with dark bordering on tergite 8 indicate large penile retractor muscles. Anal operculum with median white blotch and a few small, sharp denticles. *Venter* (Fig. 49): Labrum curved dorsally with a pair of lateral subterminal tubercles. Genital operculum and sternites yellowish with a few darker markings, usually sigilla. Operculum and sternites



Figures 48–51.—Dorsal and ventral perspectives of *Leiobunum hoffmani* new species, male holotype, female paratype. Scale bar = 1 mm.

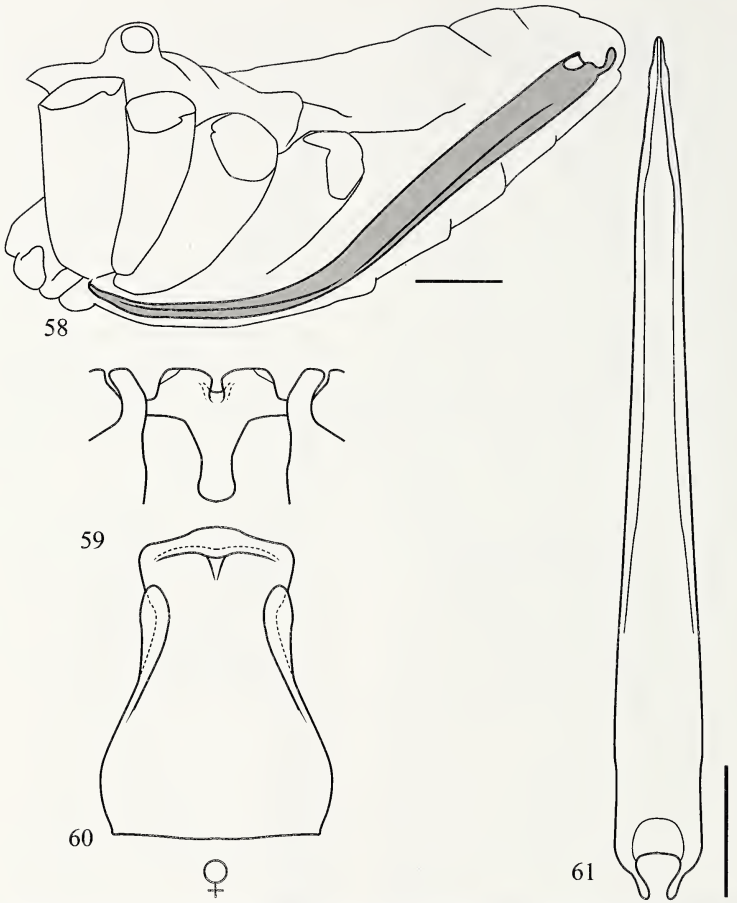
2 and 3 completely fused; demarcation between operculum and sternite 3 perceptible only as variation in color, with a short, shallow transverse fold indicating intersternal margins. Anterior margin of genital operculum strongly rebordered, with resulting "lip" protruding medially, folding over the penis tip; inner (dorsal) surface of "lip" with medial indentation. Pointed dark denticles form a lateral imperfect row; small rounded denticles and setae scattered on medial ventral surface. Supraopecular sternite simple. Sternites 3 – 7 + 8 smooth with a few short erect setae; each anterior sternite overlaps the posterior sternite; sternites 7 and 8 fused, but demarcated laterally by short transverse folds in the cuticle.

Appendages: *Chelicerae*: Dark brown, lighter on distal half of second article. Proximal segment with a few setae along distal margin. Second article with a band of short, dark, transverse stripes on proximal 3/4 of lateral and dorsal surfaces; dorsal surface with numerous erect setae, denser just proximal to fixed finger. Movable and fixed fingers dark; fixed longer.



Figures 52–57.—Right palps of *Leiobunum hoffmani* new species: 52, 53. Male holotype; 54, 55. Male variant from Grayson County, Virginia; 56, 57. Female paratype. Retrolateral perspective on left, prolateral perspective on right. Scale bar = 1 mm.

Palps (Fig. 52, 53): Measurements in mm: femur 1.6; patella 0.6; tibia 1.2; tarsus 1.7. Cuticle dark brown, proximal surface of femur and distal tip of tarsus slightly lighter. Trochanteral tubercle with a few setae and denticles. Femur narrow basally, inflated and arched distally forming a ventral concavity; large conical apophysis (0.8 mm) projects from subterminal retrolateral surface; large, a field of sharp denticles extends over the anterior apophysis surface to the distoretrodorsal margin; two imperfect longitudinal rows of sharp denticles extend along the distodorsal surface and a few large denticles form a proximal prolateral row. Erect setae scattered on ventroproximal and apophysis anterior surfaces. Patella short, robust, with scattered erect setae in longitudinal retrodorsal and prodorsal bands; proximal retrolateral margin and distal dorsal margin each with a cluster of large denticles; distal prolateral surface slightly protuberant. Tibia robust; proximal ventral surface forming flat, anvil-like prominence covered in large, proximally pointing denticles and a few long, curved setae; tibia arches to form a large ventral concavity distal to prominence; proximodorsal surface inflated, coming into apposition with the distodorsal surface of patella; 9 recurved denticles form a proventral row. Widely spaced, long, erect setae cover all but proximodorsal surface, setae especially long in ventral concavity; distal margin of tibia with short, recumbent setae. Tarsus slightly inflated proximally; curved ventrally, with distal end slightly curved retrolaterally; flat-topped tarsal denticles in highly organized tightly packed row extend nearly full length of tarsus, denticles smaller distally;



Figures 58–61.—Genital structures of *Leiobunum hoffmani* new species: 58. Diagrammatic lateral perspective of male showing position of penis; 59. Ventral perspective of female sternum (genital operculum removed); 60. Dorsal (internal) perspective of female genital operculum; 61. Dorsal perspective of penis. Figs. 59–61 to same scale. Scale bars = 1 mm.

cuticle covered with long, erect setae loosely arranged in rows, and dense coat of short, recumbent setae. Tarsal claw with 4 or 5 teeth.

Legs: Measurements of femur, patella, tibia, metatarsus, tarsus in mm: I: 6.0, 1.6, 5.9, 6.6, 8.8; II: 12.1, 2.0, 12.3, 16.3, 23.0; III: 6.4, 1.5, 5.2, 8.1, 10.1; IV: 12.4, 1.9, 12.7, 12.3, 22.5. Row of flat, evenly-spaced denticles developed along distal anterior surface of coxae I and II and along distal posterior surface of coxa IV; coxa II with 1–2 denticles on posterior margin; coxa II–IV with scattered rounded denticles on distal ventral surface; all coxae golden with scattered erect setae and a ventral submarginal row of smaller denticles and setae. Trochanters golden-brown with small, distally pointing, dark, prolateral and retrolateral denticles and a distoventral row of submarginal denticles. Femora with basal piece defined by a circumferential groove; basal piece and immediately adjacent region of shaft concolorous with coxae or nearly so; shaft brown and increases in diameter distally; sharp, distally curved denticles, each typically accompanied by a distally adjacent erect seta, densely scattered on femur I and forming loose rows on femora II–IV; ventral surface smooth except for a distoventral submarginal row of denticles. Patellae dark brown with numerous small, sharp denticles, larger distodorsally, some accompanied by distal erect setae, often arranged in imperfect rows (much reduced on leg II). Tibiae slightly increased in diameter distally with numerous sharp, distally curved denticles (reduced on leg II, especially distally) and longitudinal rows of erect setae; vestiture of microtrichia

distally; tibia II with fine circumferential stripes (pseudoarticulations) and recumbent setae. Metatarsi with a coat of fine recumbent setae, denser dorsally, and 5–7 rows of short erect setae. Metatarsi I with 5–6 pseudoarticulations, II with 10, III with 5–6, IV with 8; each psuedoarticulation with a pair of ventral spines (reduced on metatarsi II). Tarsi with long, erect setae and recumbent setae, denser distally, especially on the ventral surface where it forms a scopula-like structure; a pair of long spines developed on distoventral margin of longer (proximal) tarsomeres. Claw curved, smooth with a single ventral, tooth-like protuberance at base.

Penis (Figs. 58, 61): 6.7 mm. Lanceolate, tapering gradually, and eurving dorsally; dorsoventrally flattened at base, becoming somewhat rounder and more heavily sclerotized distally; slight lateral ridges extending the length of the shaft becoming somewhat more prominent distally. Glans flat dorsally and slightly curved; no distinct joint between glans and shaft, but ventral surface of shaft less sclerotized; stylus short compared to other species in the group and angled posteriorly. Penial fulturae nearly the length of the shaft and fused; weak medial sclerotization distally along fusion.

Variation in male.—Dorsal coloration varies greatly, with some displaying a more *calcar*-like coloring of predominantly light brown to orange with or without an apparent central figure, while others are highly patterned, with dark brown and white spotting on both the carapace and opisthosoma and a prominent central figure extending from ocularium to preanal tergite. The number and symmetry of carinal denticles varies and may encircle the eye or be present only dorsally. The most signifieant palpal variation is the greatly reduced male femoral apophysis observed in one Virginia population (Figs. 54, 55), present as only a raised protuberance, but with denticles developed along the anterior surface and distally to the femur margin, an arrangement similar to that of populations with large apophyses. Demarcation of the posterior margin of the genital operculum/sternite 2 and anterior margin of sternite 3 ranges from an incomplete transverse fold or groove to simply a variation in color. Sternites 7 and 8 may be completely fused or distinguished by a short transverse fold at the lateral margins. The tubercles of the supracheliceral lamina may be widely spaced or concentrated at the anteromedial end. Denticle rows on anterior coxa I and posterior coxa IV nearly the full length of the coxa; all other denticle rows extend half the length of each coxa or less, or may be completely absent.

Description of female paratype.—Body length: 7.6 mm. *Dorsum* (Fig. 50). Carapace length, width: 1.9 mm, 3.3 mm. Propeltidium with dark brown sigilla separated by white; lateral margin brown; surface finely granulate; anteromedian preocular prominence with 5 scattered denticles; ozopore mound with anterior and posterior denticles and a few anterior setae. Supracheliceral lamina smooth, projecting slightly, sides converging slightly. Ocularium weakly canaliculate, but appearing strongly canaliculate due to dark brown coloration with black circumocular ring; left carina with 5 sharp, curved denticles, right carina with 9 denticles. Mesopeltidium with dark brown transverse band bordered by anterior and narrow posterior white bands connected by a thin median bridge of white; bands indistinct laterally. Metapeltidium dark brown medially with a row of white spots (anterior portion of central figure), mottled brown and white laterally with a few large white spots. Opisthosoma: Distinct, dark, but transversely broken, longitudinally variable central figure most prominent on the scutum (tergites 1–5), darkest on tergites 1, 4 and 5, and represented by a pair of large dark anterior spots on remaining tergites. Scutal tergites transversely demarcated by white posterior bordering and dark brown, thin sigillary lines and small dots. Imperfect transverse rows of white dots extend across each tergite, restricted to central figure on anterior tergites. Cuticle lateral to central figure predominately whitish, darker on posterior tergites, often interrupted by brown transverse bands extending from central figure. Anal operculum with scattered, dark-tipped spines; white medially surrounded by brown margin.

Venter (Fig. 51): Labrum straight with scattered minute tubercles; at midpoint, slightly expanded laterally. Tergites light brown, fading anteriorly, with whitish posterior and lateral bordering; dark longitudinal pleural band appearing continuous with dark, transverse sigillary lines between sternites. Sternite 7 + 8 lighter medially with four brown dots arranged in two rows. Sternites 2 and 3 fused; genital operculum and all other sternites distinct. Anterior genital operculum bilobed and rebordered, forming a broad white "lip" with a posterior transverse sulcus, inner (dorsal) surface with corresponding phragma and median septum (Fig. 60). Medial surface whitish with scattered setae (denser anteriorly) and weak denticles; brown laterally, becoming 2 large brown posterior spots; submarginal row of denticles (larger anteriorly) developed laterally. Lateral margins with prominent interior anterodorsally projecting apophyses that engage the posterodorsal surface of the sternum when operculum closed. Anterior sternal margin with large, rounded median notch (to sternum midpoint) between a pair of plate-like lobes; robust posterior median process with tendinous apodemes attached laterally comprises half the total operculum length.

Appendages: *Chelicerae*: Cuticle light brown. Basal article with a row of erect setae along dorsal surface curving laterally and terminating distally at a submarginal row of erect setae; a few scattered setae ventrally. Second article with scattered erect setae on dorsal and prolateral surface; prolateral setae denser distally.

Palps (Figs. 56, 57): Measurements in mm: femur 1.4; patella 0.7; tibia 1.1; tarsus 1.7. Cuticle light brown, patella and distal ends of femur and tibia slightly darker. Trochanter with a distal prolateral row of erect setae extending from dorsal to ventral surface. Femur with proventral and retroventral rows of sharp spines, arising close together proximally and diverging distally toward the pro- and retrolateral condyles of the femur-patella joint; a few denticles scattered on subterminal dorsal surface and 4 or 5 denticles form a short imperfect proximal prolateral row; surface with scattered erect setae, especially numerous and elongate on ventral surface. Patella with setose process projecting distally from distal prolateral surface; scattered erect setae and small, distally curved sharp denticles cover all but the ventral surface; spines especially well developed near dorsal condyle of patella-tibia joint. Tibia with scattered erect setae and coat of fine recumbent setae; broad band of dark, distally projecting on ventro-proximal and ventro-retrolateral surfaces; a few well-developed spines on the distal prolateral surface. Tarsus with numerous long, erect setae, sometimes arranged in longitudinal rows, and a coat of fine recumbent setae that is especially dense on distoventral surface. Claw with 6 teeth.

Legs: Measurements of femur, patella, tibia, metatarsus, tarsus in mm: I: 6.1, 1.6, 5.1, 6.6, 6.4; II: 10.6, 1.6, 9.9, 10.5, 21.5; III: 6.2, 1.6, 4.7, 7.5, 7.9; IV: 9.0, 1.7, 7.0, 11.3, 12.6. Cuticle light brown, slightly darker on femur, patella and distally on tibia; light markings on trochanter. All coxae smooth with scattered, erect setae and a ventral submarginal row of small rounded denticles more developed anterior. Coxa I, II and III with distal anterior row of denticles and proximodorsal marginal projection; coxa IV with distal posterior row of denticles. Trochanters with small, sharp, distally pointing dark denticles scattered on prolateral and retrolateral surfaces and in a distoventral submarginal row; darker, medial groove dorsad.

Femora basal piece defined by a circumferential groove, 1–2 rows of denticles circling; femoral shaft with 5–8 imperfect rows of sharp, distally curved denticles; each denticle typically accompanied by a distally adjacent erect seta; ventral surface smooth; sharp denticles along distal margin. Patellae with small, distally curved, sharp denticles arranged in 2 rows of 6–7 dorsally, scattered proximally on ventral surface; sharp denticles on distal margin (reduced on patella II); erect setae scattered ventrad. Tibiae increase in diameter distally; surface with recumbent setae and longitudinal rows of erect setae; 5 proximal rows of distally curved denticles accompanied distally by erect setae (denticles reduced on tibia II); proximal denticles scattered ventrally; tibia II, III, IV with sharp denticles on distal margin; vestiture of microtrichia present, more dense distally; tibia II with fine, imperfect and incomplete circumferential light stripes. Metatarsus with 4–7 pairs of ventral spines; spine pairs 2–5 with increasing evidence of pseudoarticulation, but none complete; surface with scattered erect setae in loose rows and denser coat of short recumbent setae. Tarsus typical. Claws without teeth.

Ovipositor: Typical; two spermathecae present between segments 6 and 7.

Variation in female.—The median septum on the inner surface of the genital operculum ranges from short (but not absent) to very long, in some, extending nearly a third the length of the operculum and terminating with a long transverse ridge subequal in length to the anterior phragma. Fusion of sternites 2 and 3 may be incomplete. Dorsal coloration and patterning around the central figure varies, although the patterns are often more developed than on other species in the group. White bordering on the sternites may be more or less apparent. Legs, chelicerae, and palps often have similar coloration but range from light golden brown to dark brown. As with the male, the number and symmetry of carinal spines varies. The labrum surface may be smooth with a few scattered tubercles or rough from the presence of many tiny tubercles

Distribution.—The species appears to be limited to the Blue Ridge Mountains of northwestern North Carolina and southwestern Virginia (Fig. 47).

Remarks.—*Leiobunum hoffmani* shares several features with populations of *L. calcar* from the southern Appalachian Mountains, including males with very robust palps and elongate penes with reduced alae and females with very well-developed sterno-opercular mechanisms. However, *L. hoffmani* differs consistently from *L. calcar* in the simplification of the subterminal region of the penis (complete loss of alae and associated dorsal curvature) and the complete elimination of the retrolateral apophysis on the palpal femur of the female. The latter is particularly notable because there is a clear tendency for females in the montane *L. calcar* to have larger apophyses.

ACKNOWLEDGMENTS

We thank Jason Weintraub (ANSP), Dana DeRoche (NMNH), Laura Leibensperger (MCZ), Lorenzo Prendini and Jeremy Huff (AMNH), and Richard Hoffman (VMNH) and Rowland Shelley (NCMNS) for providing access to material in their care, and Marshal Hedin, Matt Sarver, Bob Smith, Pat Miller, Gail Stratton, and Bob Suter for collecting specimens. We thank two anonymous referees for their helpful comments. EAI was supported by a Gahan Graduate Fellowship from the Department of Entomology, University of Maryland, and JWS was supported by the Maryland Agricultural Experiment Station. This work funded by National Science Foundation grant DEB-0640179.

LITERATURE CITED

Banks, N. 1893. The Phalanginae of the United States. Canadian Entomologist 25:205–211.

Banks, N. 1894. The Phalangida of New York. Journal of the New York Entomological Society 2:40–41.

Banks, N. 1901. Synopses of North-American invertebrates. XVI. The Phalangida. American Naturalist 35:669–679.

Bishop, S.C. 1949. The Phalangida (Opiliones) of New York. Proceedings of the Rochester Academy of Sciences 9:159–235.

Carter, N.E. & N.R. Brown. 1973. Seasonal abundance of certain soil arthropods in a fenitrothion-treated red spruce stand. Canadian Entomologist 105:1065–1073.

Cokendolpher, J.C. 1981. Status of *Leiobunum serratipalpe* Roewer (Opiliones, Leiobunidae). Journal of Arachnology 9:112–113.

Cokendolpher, J.C. & V.F. Lee. 1993. Catalogue of the Cyphopalpatores and bibliography to the harvestmen (Arachnida, Opiliones) of Greenland, Canada, USA and Mexico. Vintage Press, Lubbock, Texas.

Crosby, C.R. 1904. Notes on some phalangids collected near Ithaca, N.Y. Journal of the New York Entomological Society 12:253–256.

Crosby, C.R. & S.C. Bishop. 1924. Notes on the Opiliones of the southeastern United States with descriptions of new species. Journal of the Elisha Mitchell Scientific Society 40:8–26.

Davis, N.W. 1934. A revision of the genus *Leiobunum* (Opiliones) of the United States. American Midland Naturalist 15:662–705.

Edgar, A.L. 1966. Phalangida of the Great Lakes Region. American Midland Naturalist 75:347–366.

Edgar, A.L. 1971. Studies on the biology and ecology of Michigan Phalangida (Opiliones). Miscellaneous Publications, Museum of Zoology, University of Michigan No. 144, 1–64.

Edgar, A.L. 1990. Opiliones (Phalangida). Pp. 529–581. *In* Soil Biology Guide. (D.L. Dindal, ed.). Wiley, New York.

Hackman, W. 1956. Phalangida (Opiliones) from Newfoundland. Societas Scientiarum Fennica. Commentationes Biologicae 15:1–9.

Hedin, M., N. Tsurusaki, R.Macías-Ordóñez & J.W. Shultz. In press. Molecular systematics of sclerosomatid harvestmen (Opiliones Phalangioidea, Sclerosomatidae): geography is better than taxonomy in predicting phylogeny. Molecular Phylogenetics and Evolution.

Holmberg, R.G. 1999. Harvestmen (Arachnida, Opiliones) of Alberta, Saskatchewan and Manitoba [Abstract]. Proceedings of the 46th Annual Meeting of the Entomological Society of Alberta 46:11.

Jennings, D.T., M.W. Houseweart & J.C. Cokendolpher. 1984. Phalangids (Arachnida: Opiliones) associated with strip clearcut and dense spruce-fir forests of Maine. Environmental Entomology 13:1306–1311.

Katayama, R.W. & R.L. Post. 1974. Phalangida of North Dakota. North Dakota Insects No. 9, 1–40.

Levi, L.R. & H.W. Levi. 1952. Preliminary list of harvestmen of Wisconsin with a key to genera. Transactions of the Wisconsin Academy of Sciences, Arts and Letters 41:163–167.

McGhee, C.R. 1970. The sacculate and lanceolate groups of the genus *Leiobunum* (Arachnida, Phalangida, Phalangiidae) in the eastern United States. Unpublished doctoral dissertation, Department of Zoology, Virginia Polytechnic Institute and State University, Blacksburg, Virginia.

Roewer, C.F. 1910. Revision der Opiliones Plagiostethi (= Opiliones Palpatores). I. Teil: Familie der Phalangiidae. (Subfamilien: Gagrellini, Liobunini, Leptobunini). Abhandlungen des Naturwissenschaftlichen Vereins in Hamburg 19(4):1–294.

Roewer, C.F. 1923. Die Weberknechte der Erde. Systematische Bearbeitung der bisher bekannten Opiliones. Gustav Fischer, Jena.

Walker, M.E. 1928. A revision of the order Phalangida of Ohio. Ohio Biological Survey, Bulletin 19:149–175.

Weed, C.M. 1887. The genera of North American Phalangiinae. American Naturalist 21:935.

Weed, C.M. 1889a. A descriptive catalogue of the Phalangiinae of Illinois. Bulletin of the Illinois State Laboratory of Natural History 3:79–97.

Weed, C.M. 1889b. A partial bibliography of the Phalangiinae of North America. Bulletin of the Illinois State Laboratory of Natural History 3:99–106.

Weed, C.M. 1890. The harvest spiders of North America. American Naturalist 24:914–918.

Weed, C.M. 1892. Descriptions of new, or little-known North American harvest-spiders (Phalangiidae). Transactions of the American Entomological Society 19:187–194.

Weed, C.M. 1893a. A descriptive catalogue of the harvest-spiders (Phalangiidae) of Ohio. Proceedings of the United States National Museum 16:543–563.

Weed, C.M. 1893b. A synopsis of the harvest-spiders (Phalangiidae) of South Dakota. Transactions of the American Entomological Society 20:285–292.

Wood, H.C. 1868. On the Phalangeae of the United States of America. Proceedings of the Essex Institute 6:10–40.

Manuscript received 12 May 2011, revised 19 September 2011.

2011. The Journal of Arachnology 39:482–489

New species and new records of jumping spiders (Araneae: Salticidae: Heliophaninae) from the Lake Victoria area

Wanda Wesołowska: Institute of Zoology, Wrocław University, Sienkiewicza 21, 50-335 Wrocław, Poland. E-mail: tomwes@biol.uni.wroc.pl

Abstract. Four new species of salticids from the neighborhood of Lake Victoria in eastern Africa are described: *Heliophanus jacksoni*, *Icius mbitaensis*, *Pseudicius athleta* and *Pseudicius roberti*. *Icius steeleae* Logunov 2004 is recorded for the first time in Uganda.

Keywords: Jumping spiders, new species, Afrotropical Region

Although studies of Afrotropical jumping spiders have been intense in recent years, the diversity of salticids of most parts of this region is still poorly known. Over 70 species of salticids are known from Kenya (Platnick 2011; Prószyński 2011). This number looks quite impressive, but the western part of this country remains almost completely unstudied. Robert Jackson and his team collected numerous salticids during a long-term behavioral survey of jumping spiders conducted on the northeastern shore of Lake Victoria in Kenya. A few of these species have been formally described; e.g., *Myrmarachne melanotarsa* Wesołowska & Salm 2002, *Evarcha culicivora* Wesołowska & Jackson 2003 and *Menemerus tropicus* Wesołowska 2007. Descriptions of four additional Kenyan salticids from this collection are given in the present paper. The behavior of two of those species was studied by Jackson (1986); they were reported provisionally as *Pseudicius* sp. 1 (in the present paper *Pseudicius athleta*) and *Pseudicius* sp. 2 (now *Icius mbitaensis*). These are unusual colonial salticids, which live in large interspecific aggregations within the web complexes of araneids (Jackson 1986).

Occasionally spiders were also collected by the same team on the north shore of Lake Victoria in Uganda. This collection yielded records of four new species for this country; including the earlier described *Parajotus cinereus* Wesołowska 2004 and *Ugandinella formicula* Wesołowska 2006. This increases the total number of species known form Uganda from eleven (Prószyński 2011) to thirteen.

METHODS

Specimens were examined in a dish with 75% ethanol. Descriptions of colors pertain to wet specimens. The drawings were made with the aid of a reticular eyepiece attached to a Nikon SMZ stereomicroscope. The epigynes and the male pedipalps were removed for study. The epigynes were macerated in hot 5% KOH for a few minutes, and cleared in eugenol. After drawings, the genitalia were placed in micro-vials with ethanol and put into the vials containing the specimens from which they been removed. All measurements are given in millimeters. Digital photos were taken of each salticid species using a Nikon Coolpix 8400 mounted on a Nikon SMZ stereomicroscope. The extended focal range images were stacked using CombineZM image stacking software (http://www.hadleyweb.pwp.blueyonder.co.uk) to increase the depth of field. Figures were prepared in Photoshop 7.0.

Voucher specimens have been deposited in the Florida State Collection of Arthropods, Gainesville, Florida, USA (FSCA) and the Royal Museum for Central Africa, Tervuren, Belgium (MRAC).

TAXONOMY

Heliophanus (Helafricanus) jacksoni new species
Figs. 1–6

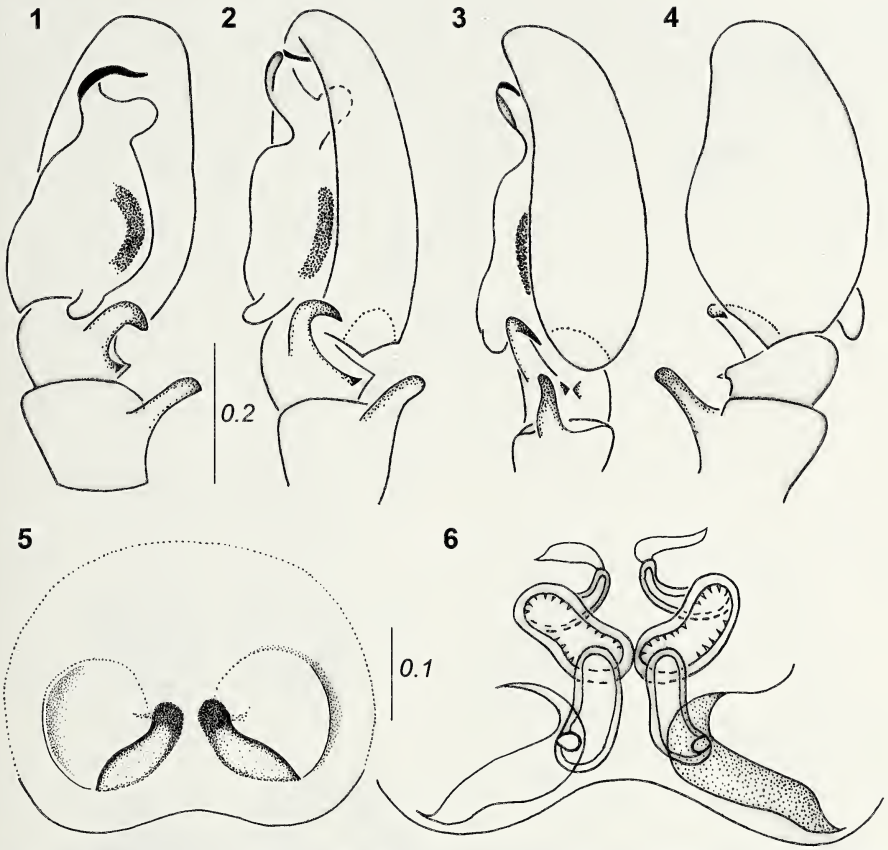
Type material.—Male holotype, KENYA: Mbita Point, shore of Lake Victoria (0°25′S, 34°13′E, 1150 m), December 2002, leg. R. Jackson (FSCA, K 191/02); 3 male and 2 female paratypes: same data as holotype, (FSCA); 1 male and 1 female paratypes: same data as holotype (MRAC); 1 male and 5 female paratypes: same locality, December 1997 (FSCA); male paratype: same locality, tree trunk, January 2003 (FSCA).

Diagnosis.—This species is closely related to *Heliophanus xanthopes* Wesołowska 2003 from Ethiopia. The male is distinguishable by the blunt patellar apophysis of the palp (pointed in *H. xanthopes*), more curved embolus and larger lobe at base of embolus (compare Fig. 1 herein with fig. 138 in Wesołowska 2003). The female has characteristic weakly sclerotized epigyne with translucent atria enveloping gonopores.

Etymology.—This species is named after Robert Jackson, collector of the type material and expert in behavior of salticids.

Description.—Measurements (male/female) [in mm]. Cephalothorax: length 1.3–1.6/1.6–1.8, width 1.0–1.2/1.3–1.4, height 0.5–0.6/0.6. Abdomen: length 1.2–1.5/2.5–3.1, width 0.9–1.1/1.9–2.1. Eye field: length 0.5–0.6/0.6–0.7, anterior width 0.8–1.0/1.0–1.1, posterior width 0.9–1.1/1.1–1.2.

Male. Small, dark colored spider. Carapace dark brown, eye field trapezoid, iridescent, pitted. Long brown bristles near eyes, minute setae on thoracic part. Mouthparts and sternum brown. Abdomen oval, dark brown, venter brownish gray. White hairs form thin median light line extending along thoracic part of carapace and abdomen. Legs yellow, contrasting with dark body, bearing brown hairs and spines. Pedipalps brown. Patellar apophysis straight, with blunt tip. Tibia with three apophyses, largest of them hooked, placed ventrally at distal end of tibia; two others very short. Cymbium with small retrolateral depression at base, corresponding to longest tibial apophysis (Figs. 1–4). Embolus bent



Figures 1–6.—*Heliophanus jacksoni* sp. n. 1. Palpal organ, ventral aspect; 2. Palpal organ, ventrolateral aspect; 3. Palpal organ, lateral aspect; 4. Palpal organ, dorsal aspect; 5. Epigyne; 6. Internal structure of epigyne.

toward bulb, bulb with large rounded lobe near base of embolus (Figs. 1, 2).

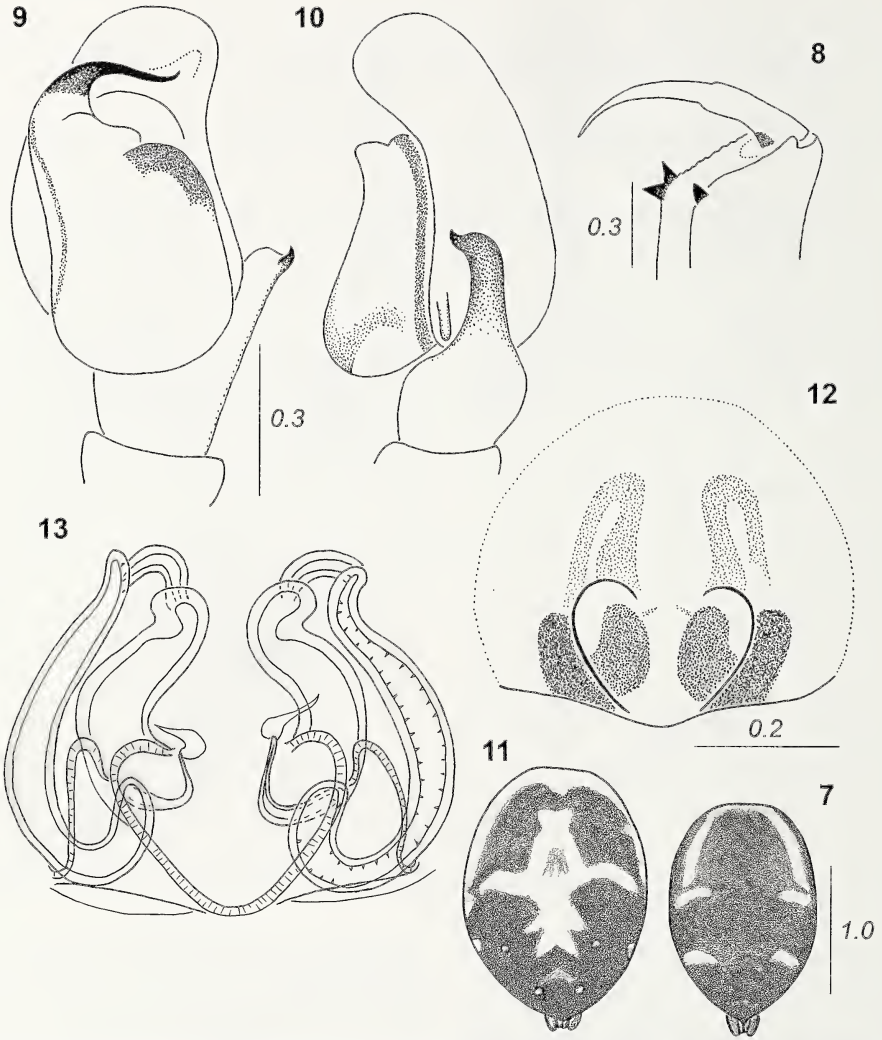
Female. Slightly larger and lighter colored than male. Carapace oval, brown, eye field slightly darker, eyes surrounded by black rings. Some long bristles near eyes, a few white scales at eyes of first row, short grayish hairs on carapace. Chelicerae light brown, sternum darker, endites and labium dark yellow. Abdomen ovoid, dark brownish with lighter median belt composed of five pairs of lighter spots. Thin light band on anterior margin spreading to sides, venter light, tinged with gray or with broad dark streak. Spinnerets beige. Legs yellow, sometimes with brownish rings on both ends of segments. Epigyne weakly sclerotized, with two very shallow round depressions (Fig. 5). Gonopores placed in deep, heavily sclerotized, inner posterior part of the atria, seminal ducts short (Fig. 6).

Distribution.—Known only from the type locality.

Remarks.—This species belongs to the *crudeni* species group (Wesołowska 1986).

Icius mbitaensis new species
Figs. 7–13, 33

Type material.—Male holotype, KENYA: Mbita Point, shore of Lake Victoria (0°25′S, 34°13′E, 1150 m), December 1998, leg. R. Jackson (FSCA, K 10/98): 1 male and 7 female paratypes, same data as holotype (FSCA); female paratype, same locality, February 1996 (FSCA); 4 female paratypes, same locality, February 1998 (FSCA); 3 female paratypes, same locality, January 1998 (FSCA); male paratype, same locality, May 2001 (FSCA); 2 male paratypes, same locality, January 2003 (FSCA); 2 male and 6 female paratypes, same locality, January 2003 (MRAC).



Figures 7–13.—*Icius mbitaensis* sp. n. 7. Abdominal pattern of male; 8. Cheliceral dentition of male; 9. Palpal organ, ventral aspect; 10. Palpal organ, lateral aspect; 11. Abdominal pattern of female; 12. Epigyne; 13. Internal structure of epigyne.

Diagnosis.—This species is closely related to *Icius steeleae* Logunov 2004. The male differs in having a shorter tibial apophysis of palp (in the latter species apophysis is extremely long, equal to bulb length), smaller cymbial tutaculum (ear-shaped apophysis), and longer, curved embolus (compare Figs. 9, 10 with Figs. 14, 15). The female has epigynal pocket as long as epigynal depression (clearly shorter in *I. steeleae*), longer seminal ducts, and longer and thinner spermathecae (compare Figs. 12, 13 with Figs. 18–20).

Etymology.—Named after the type locality.

Description.—Measurements (male/female). Cephalothorax: length 2.1–2.2/2.0, width 1.6/1.6, height 0.6/0.6. Abdomen: length 2.3/2.2–2.7, width 1.3/1.4–1.5. Eye field: length 0.9/0.9, anterior width 1.2/1.2, posterior width 1.3/1.3.

Male. Small, elongated spider with flat body (Fig. 33). Carapace oval, flattened, brown with slightly darker iridescent pitted eye field, eyes surrounded with black area, some long brown bristles at first row of eyes. Thoracic part of carapace clothed in translucent hairs, white hairs form thin line along lateral carapace margins. Chelicerae dark brown, unidentate (Fig. 8). Labium and endites dark brown, sternum lighter. Abdomen ovoid, brownish gray, sometimes with light lateral streaks extending from anterior edge to its middle and with traces of two pairs of transverse patches (Fig. 7). Dorsal surface of abdomen covered with short translucent hairs and brown bristles. Venter light, tinged with gray. Spinnerets brownish. Legs yellow, first pair brown, longer and stouter than others. Pedipalps brown, their femora slightly swollen, tibial apophysis wide with curved pointed tip, bulb oval, embolus bent toward bulb (Figs. 8, 9). Cymbium with small retrolateral tutaculum at base.

Female. Similar to male. Carapace covered with dense short gray hairs, with wide white streaks along lateral margins extending to clypeus. Abdomen brown, in some specimens reddish brown anteriorly, sometimes with light pattern composed of light band on anterior margin extending to sides, large median patch and two pairs of small rounded spots in posterior part (Fig. 11). First leg not stouter than others. Epigyne with heart-shaped depression and large pockets at epigastric fold to either side of depression (Fig. 12). Internal structure as in Fig. 13, spermathecae very long and thin.

Distribution.—Known only from the type locality.

Natural history.—The species (= *Pseudicius* sp. 2 in Jackson 1986) lives communally in large interspecific nest aggregations within the web complexes of araneids. The males perform vibratory courtship at nests and visual courtship away from them. They cohabit with subadult females in nests and mate with them when they are mature (Jackson 1986).

Icius steeleae Logunov 2004
Figs. 14–20, 34

Icius steeleae Logunov 2004:86.

Material examined.—UGANDA; Entebbe (0°04′N, 32°28′E), 14 males, 27 females, 4 imm., January 1996, leg. R. Jackson (FSCA); same data, 1 male, 1 female (MRAC); same locality, February 1996, 5 males, 7 females, 2 imm., February 1996; Mweya, E shore of Lake Edward (0°12′S, 29°52′E), in vegetation 1 male, 2 females, January 1996, leg. R. Jackson (FSCA).

Diagnosis.—see under *I. mbitaensis*.

Redescription.—Measurements (male/female). Cephalothorax: length 2.0/1.9, width 1.4/1.4, height 0.6/0.6. Abdomen: length 2.2/2.4, width 1.2/1.5. Eye field: length 0.9/0.9, anterior width 1.1/1.2, posterior width 1.2/1.3.

Male. General appearance as in Fig. 34. Carapace oval, flattened, dark brown, eyes surrounded with black rings. Eye field with metallic luster, pitted. Short translucent and grayish hairs cover carapace, longer brown bristles near eyes, thin line formed with white hairs along lateral margins of carapace. Clypeus not expressed. Anterior median eyes fringed with orange fawn scales. Mouthparts and sternum brown, endites with large lateral lobes. Abdomen oval, yellowish fawn, venter light with two thin darker lines. Delicate hairs on abdominal dorsum. Spinnerets light brown. First pair of legs slightly longer and thicker than others, brown with lighter distal segments. Other legs yellow. Spines and leg hairs brown. Pedipalps with swollen femur (Fig. 16). Tibial apophysis very long and wide, cymbium with big retrolateral tutaculum at base (Figs. 14, 15).

Female. Similar to male, coloration slightly lighter. White streaks along carapace margins broader. Sternum with dark patch in center, endites with whitish chewing margins. Abdomen yellow with delicate brownish pattern (Fig. 17). Legs yellow. Some specimens darker colored, with whole body brown. Epigyne strongly sclerotized, with heart-shaped central depression and clearly visible big lateral pockets (Figs. 18, 19). Internal structure as in Fig. 20, accessory glands small, spermathecae elongated.

Distribution.—The species hitherto known only from western Sudan, for the first time recorded in Uganda.

Pseudicius athleta new species
Figs. 21–26, 32

Type material.—Male holotype, UGANDA: Entebbe (0°04′N, 32°28′E), January 1996, leg. R. Jackson (FSCA, U196/96): 6 male and 4 female paratypes (FSCA): 4 male and 1 female paratypes, same locality, December 1997 (MRAC); 8 male and 2 female paratypes, KENYA: Mbita Point, shore of Lake Victoria (0°25′S, 34°13′E, 1150 m), January 1998 leg. R. Jackson (FSCA).

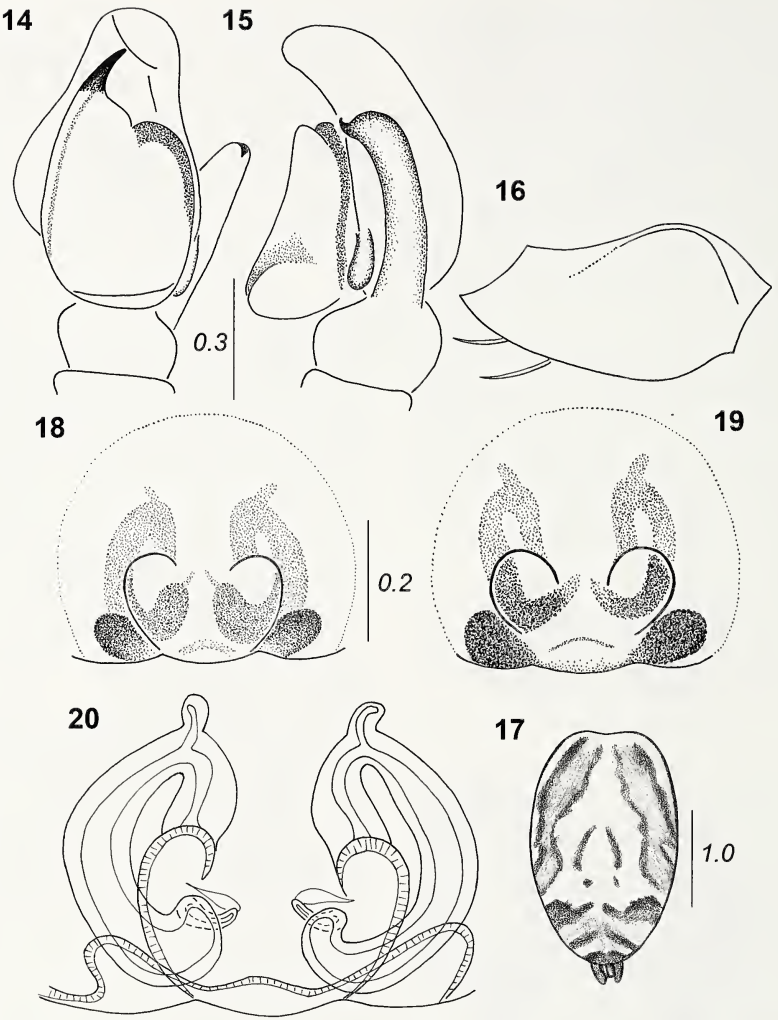
Diagnosis.—The male is distinguishable by having a very thick first pair of legs with extremely swollen tibiae. The male palpal organ resembles that of male *Pseudicius delesserti* Caporiacco 1941 from Ethiopia, but differs from it by the thinner, more delicate embolus and the shape of tibial apophysis, which has an additional proximal tooth (compare Fig. 15 herein with figure on p. 50 in Prószyński 1987). The female is distinctive, in having a unique form of epigyne with posteriorly placed copulatory openings and very narrow spermathecae.

Etymology.—From Latin, *athleta*; the specific name is a noun in apposition, an allusion to extremely swollen ("muscular") tibia of the first leg.

Description.—Measurements (male/female). Cephalothorax: length 1.8–2.2/1.9–2.2, width 1.3–1.5/1.3–1.5, height 0.6/0.6. Abdomen: length 2.4–2.8/2.2–2.8, width 1.4–1.7/1.4–1.8. Eye field: length 0.7–0.8/0.8–0.9, anterior width 0.9–1.0/0.9–1.0, posterior width 1.0–1.1/1.0–1.1.

Male. Small spider, shape of body typical for the genus, slender and flat, with powerful first pair of legs (Fig. 32). Carapace elongated, strongly flattened, dark brown with black eye field, clothed in delicate grayish white hairs, very long brown bristles near eyes. White hairs form thin median line on eye field and thoracic part, and bands along lateral margins of carapace. Mouthparts dark brown, sternum slightly lighter. Stridulatory apparatus present, composed of a row of long setae on tubercles under lateral eyes and a row of short setae on prolateral surface of first femur apically. Abdomen elongated, dorsum with wide brownish fawn median streak, sides light with two or three pairs of diagonal marginal dark patches, venter yellow. Brown and white hairs cover dorsal surface of abdomen. Spinnerets gray. First pair of legs longer than others, thick, with extremely swollen tibiae (Fig. 21). Single short thick spine on prolateral surface of tibia apically and two pairs of short ventral spines on metatarsus. First leg brown, others yellow or light brownish. Leg hairs brown, some of them very long. Pedipalps as in Figs 22, 23, tibia short, apophysis furcated with additional proximal tooth.

Female. Similar to male. Abdomen lighter, grayish beige with faint darker herring-bone pattern and traces of three



Figures 14–20.—*Icius steeleae* Logunov. 14. Palpal organ, ventral aspect; 15. Palpal organ, lateral aspect; 16. Palpal femur; 17. Abdominal pattern of female; 18, 19. Epigyne; 20. Internal structure of epigyne.

pairs of diagonal marginal patches, pair of small round white spots surrounded by black flanges posteriorly. First pair of legs not as thick as in male, but their tibiae also swollen. Epigyne with gonopores placed posteriorly (Fig. 24), seminal ducts coiled, accessory glands large, spermathecae narrow, tubuliform (Fig. 25).

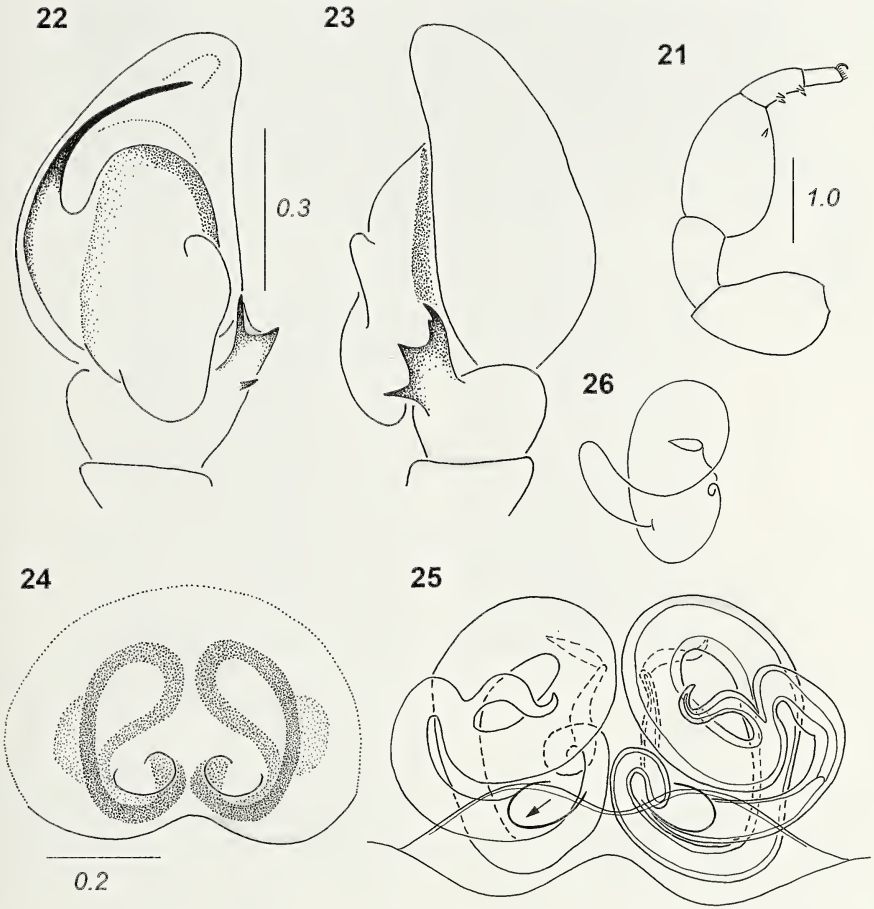
Distribution.—Kenya and Uganda.

Natural history.—Courtship and sociality of this species has been studied by Jackson (1986); the species was provisionally determined only to generic level and reported as *Pseudicius* sp. 1. Its social and mating behavior are as in *Icius mbitaensis* (see above).

Remarks.—The species belongs to the *cinctus* group of species (Prószyński 2003).

Pseudicius roberti new species
Figs. 27–31, 35

Type material.—Male holotype, KENYA: Mbita Point, E shore of Lake Victoria, (0°25′S, 34°13′E, 1150 m), February



Figures 21–26.—*Pseudicius athleta* sp. n. 21. First leg, prolateral aspect; 22. Palpal organ, ventral aspect; 23. Palpal organ, lateral aspect; 24. Epigyne; 25. Internal structure of epigyne; 26. Diagrammatic course of seminal duct.

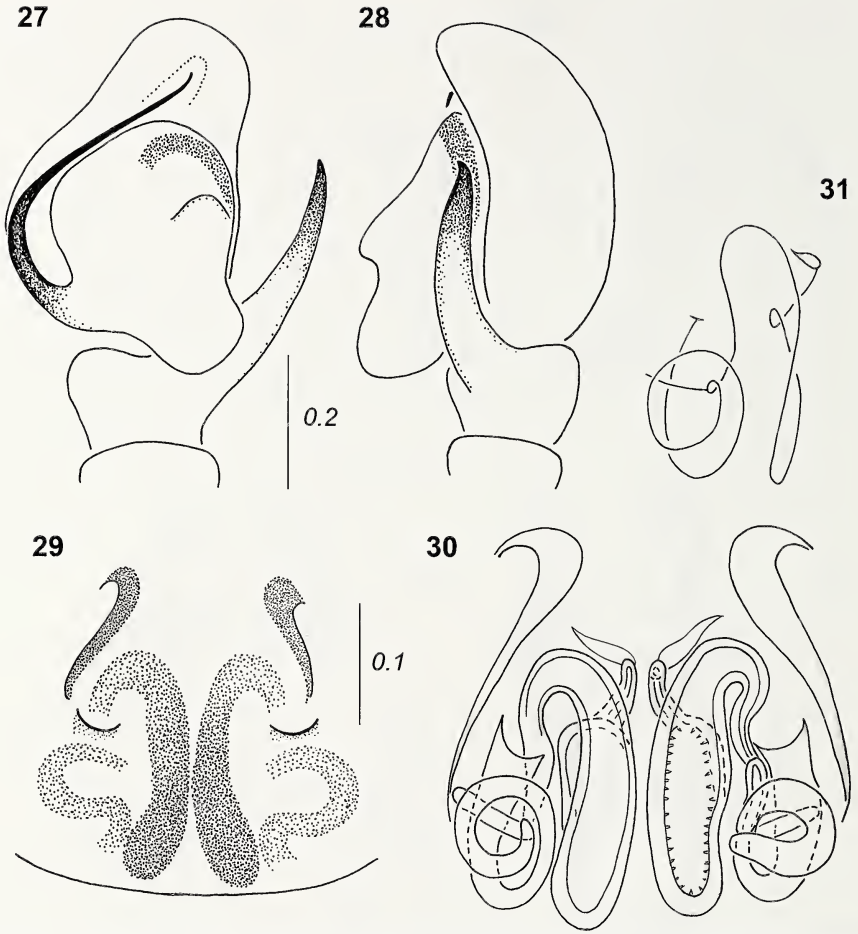
1998, leg. R. Jackson (FSCA, K815/98); 1 male and 3 female paratypes, same data as holotype (FSCA); 1 male and 3 female paratypes, same locality, January 1998 (FSCA); 11 male and 13 female paratypes, same locality, December 1997 (FSCA); 1 male and 1 female paratypes, same locality, January 2003 (MRAC).

Diagnosis.—The male of this species resembles the male of *Pseudicius eximius* Wesołowska & Russell-Smith 2000 from Tanzania, but bulb and embolus are shorter, base of embolus is placed further from posterior lobe of bulb (compare Fig. 27 herein with fig. 248 in Wesołowska & Russell-Smith 2000). The female has epigyne typical for members of the *tamaricis* group of species, but seminal ducts are narrower and shorter than in other species.

Etymology.—This species is dedicated to Robert Jackson, eminent explorer of spider behavior and collector of type specimens.

Description.—Measurements (male/female). Cephalothorax: length 1.4–1.5/1.5–1.6, width 1.0–1.1/1.1–1.2, height 0.4/0.4. Abdomen: length 1.7–1.8/1.9–2.4, width 1.1–1.2/1.2–1.4. Eye field: length 0.6/0.6, anterior width 0.8–0.9/0.8–0.9, posterior width 0.9–1.0/0.9–1.0.

Male. Very small, slender spider. Body elongated and flattened. Carapace oval, flat, dark brown with black eye field.



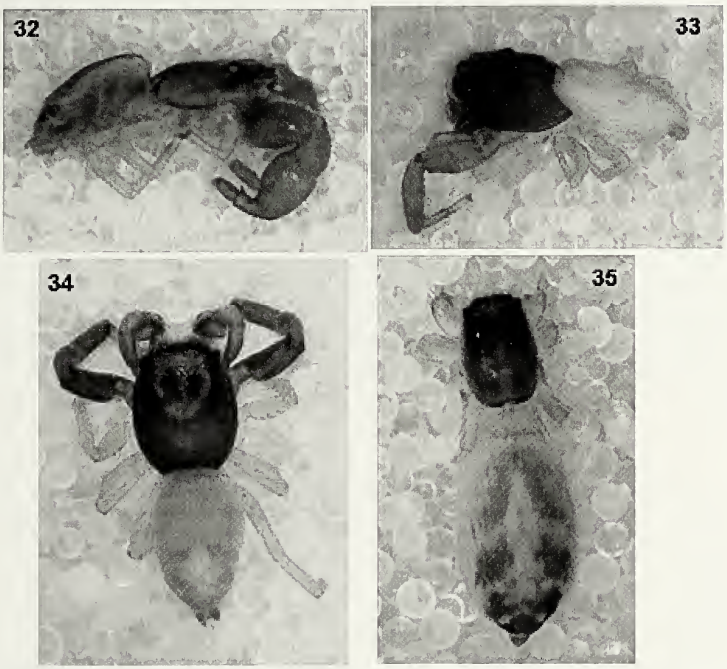
Figures 27–31.—*Pseudicius roberti* sp. n. 27. Palpal organ, ventral aspect; 28. Palpal organ, lateral aspect; 29. Epigyne; 30. Internal structure of epigyne; 31. Diagrammatic course of seminal duct.

Ocular area slightly pitted, with luster. White hairs cover carapace, denser on eye field anteriorly, also form thin median line on thoracic part and two bands along lateral margins of carapace. Anterior eyes surrounded with white scales, some brown bristles near eyes. Stridulatory apparatus present (the leg-carapace type). Mouthparts light brown, sternum dark yellow. Abdomen elongated, blackish brown with white pattern composed of two pairs of transverse submarginal patches and few faint posterior chevrons, in some specimens light bands on sides in anterior half of abdomen. Abdominal dorsum clothed in brown hairs, denser anteriorly. Venter light. Spinnerets light brown. Legs yellow, first pair stouter and longer than other, brown, with slightly swollen tibiae. Tibia with two short spines on prolateral surface, metatarsus with two pairs of ventral spines. Pedipalps light brown. Tibial apophysis very long (Figs. 27, 28).

Female. Similar to male. Abdomen with additional pair of small rounded spots at posterior margin (Fig. 35), in some specimens abdomen dark, without patches, only with two lighter lateral bands in anterior part. Epigyne with two anterior widely separated pockets (Fig. 29). Internal structure of epigyne as in Fig. 30, seminal ducts coiled, long accessory glands leading into the ducts, spermathecae large, elongated.

Distribution.—Known only from the type locality.

Remarks.—The species is members of the *tamaricis* group of species (Prószyński 2003).



Figures 32–35.—32. Male of *Pseudicius athleta*, lateral aspect; 33. Male of *Icius mbitaensis*, lateral aspect; 34. Male of *Icius steeleae*, dorsal aspect; 35. Female of *Pseudicius roberti*, dorsal view.

ACKNOWLEDGMENTS

My thanks go to Robert R. Jackson and G.B. Edwards for providing specimens for study. Dmitri Logunov and G.B. Edwards are acknowledged for their valuable comments on the earlier draft of the manuscript and linguistic help.

LITERATURE CITED

Jackson, R.R. 1986. Communal jumping spiders (Araneae: Salticidae) from Kenya: interspecific nest complexes, cohabitation with web-building spiders, and intraspecific interactions. New Zealand Journal of Zoology 13:13–26.

Logunov, D.V. 2004. Taxonomic notes on a collection of jumping spiders from Sudan (Araneae, Salticidae). Bulletin of the British Arachnological Society 13:86–90.

Platnick, N.I. 2011. The World Spider Catalog. Version 12. American Museum of Natural History, New York. Online at <http://research.amnh.org/iz/spiders/catalog>

Prószyński, J. 1987. Atlas rysunków diagnostycznych mniej znanych Salticidae. Wyższa Szkoła Pedagogiczno Rolnicza, Siedlce.

Prószyński, J. 2003. Salticidae (Araneae) of the Old World and Pacific Islands in several US collections. Annales Zoologici, Warszawa 44:87–163.

Prószyński, J. 2011. Salticidae (Araneae) of the World. Museum and Institute of Zoology, Polish Academy of Sciences, Online at <http://www.gsd-salt.miiz.waw.pl/salticidae.php>

Wesołowska, W. 1986. A revision of the genus *Heliophanus* C.L. Koch, 1833. Annales Zoologici, Warszawa 40:1–254.

Wesołowska, W. 2003. New data on African *Heliophanus* species with descriptions of new species (Araneae: Salticidae). Genus 14:249–294.

Wesołowska, W. & A. Russell-Smith. 2000. Jumping spiders from Mkomazi Game Reserve in Tanzania (Araneae: Salticidae). Tropical Zoology 13:11–127.

Manuscript received 29 July 2011, revised 23 September 2011.

2011. The Journal of Arachnology 39:490–494

Cytogenetic studies on five species of spiders from Turkey (Araneae: Gnaphosidae, Lycosidae)

Zübeyde Kumbıçak: Biology Department, Art and Science Faculty, Nevşehir University, Nevşehir, Turkey. E-mail: akanzubeyde@gmail.com

Serap Ergene: Biology Department, Art and Science Faculty, Mersin University, Mersin, Turkey

Ayla Karataş: Biology Department, Art and Science Faculty, Kocaeli University, Kocaeli, Turkey

Ümit Kumbıçak: Biology Department, Art and Science Faculty, Uludağ University, Bursa, Turkey

Abstract. The chromosome diploid number (2n) and the sex chromosome system in males of five species belonging to the families Gnaphosidae and Lycosidae were determined as 2n = 22 (20 + X_1X_2) and 2n = 28 (26 + X_1X_2), respectively. *Nomisia conigera* (Spassky 1941), *Haplodrassus morosus* (O. Pickard-Cambridge 1872) and *Haplodrassus dalmatensis* (L. Koch 1866) have 10 autosomal bivalents and two univalent sex chromosomes, while *Pardosa bifasciata* (C.L. Koch 1834) and *Arctosa cinerea* (Fabricius 1777) have 13 autosomal bivalents and two univalent sex chromosomes during first meiotic stages of prophase I and metaphase I. All species have acrocentric chromosomes and chiasmatic meiosis.

Keywords: Karyotype, meiosis, sex chromosome

Cytogenetic studies of the families Gnaphosidae and Lycosidae (Arachnida: Araneae) are scarce. From the over 4400 species of gnaphosids and lycosids, less than 4% have been cytogenetically analyzed (Chemisquy et al. 2008; Kumbıçak et al. 2009). The diploid number of chromosomes (2n) in males range from 21 to 30 in gnaphosids and 12 to 30 in lycosids (Hackman 1948; Suzuki 1954; Sharma et al. 1958; Kageyama et al. 1978; Srivasta & Shukla 1986; Painter 1914; Gorlov et al. 1995; Akan et al. 2005; Kumbıçak et al. 2009). Most of the analyzed species have only telocentric or acrocentric chromosomes; the sex chromosome system X_1X_2 ♂/ $X_1X_1X_2X_2$ ♀ occurs in 94% of lycosids (Chemisquy et al. 2008) and 99% of gnaphosids analyzed thus far. This paper reports the first results on the karyotypes and spermatogenesis of five common Turkish spider species belonging to the families Gnaphosidae and Lycosidae.

METHODS

Specimens were collected in March–June 2009 (Table 1) and deposited in the collection of Nevşehir University, Science & Art Faculty, Biology Department, Turkey. We made chromosome preparations according to the spreading technique described by Traut (1976) with some modifications. Gonads were dissected out in Ringer's solution and transferred to a hypotonic solution (0.075 KCl) for 20 min. We placed tissues in Carnoy fixative (ethanol: cloroform: glacial acetic acid; 6:3:1) for 35 min. Afterwards, they were macerated in 60% acetic acid on the surface of glass slide (surface temperature 42° C). The suspension was moved by pushing it with a tungsten needle and stained with 5% Giemsa solution in Sörensen phosphate buffer (pH = 6.8) for 30–55 min. We visualized the cells under a Soif XSZ-G microscope and photographed them with an Olympus DP 20-5E Digital Camera by DP2-BSW programme. For karyotyping, we evaluated ten spermatogonial metaphases and calculated relative chromosome lengths (RCL) and centromeric indexes (CI). Chromosome classification was determined according to Levan et al. (1964).

RESULTS

Nomisia conigera (Spassky 1941)

The karyotype of *N. conigera* consists of 22 chromosomes, including the two X chromosomes (Fig. 2a). All autosomal pairs are acrocentric and gradually decrease in size (Fig. 1a). In mitotic metaphase, the length of autosome pairs ranges from 5.38 to 10.15% (Table 2). Spermatocytes show 10 autosomal bivalents and two univalent sex chromosomes in the first meiotic division. During the leptotene and pachytene stages of prophase I, X_1 and X_2 were tightly aligned forming a so-called sex vesicle that is positively heterpycnotic (Fig. 2b). At the diplotene stage of prophase I, diakinesis and metaphase I sex chromosomes were isopycnotic (Fig. 2c).

Haplodrassus morosus (O. Pickard-Cambridge 1872)

The species possesses 22 chromosomes, including two X chromosomes (Fig. 2d). All autosomal pairs and sex chromosomes are acrocentric. Autosomes gradually decreased in size (Fig. 1b). Relative chromosome lengths of autosomal pairs are between 5.99 to 11.47% (Table 2). Relative lengths of sex chromosomes X_1 and X_2 were 10.29 and 8.61%, respectively. There is no significant difference in sex chromosomes in size (Table 2). During the leptotene stage, sex chromosomes were isopycnotic (Fig. 2e). At metaphase I, there were 10 autosomal bivalents and two isopycnotic univalents, the sex chromosomes (Fig. 2f).

Haplodrassus dalmatensis (L. Koch 1866)

The spermatogonial plates consist of 22 chromosomes (Fig. 2g). All autosomal pairs are acrocentric. Autosomes gradually decrease in size (Fig. 1c). Relative lengths of autosomal pairs range from 6.92 to 10.28% (Table 2). The karyotype contains two sex chromosomes, X_1 and X_2 (Fig. 1c). Relative lengths of sex chromosomes X_1 and X_2 are 7.55 and 6.43%. X_2 is the shortest chromosome in the karyotype. During the first meiotic division, sex chromosomes are heavily stained until the end of diakinesis (Fig. 2h). Two types of anaphase II plates were observed with 10 or 12 chromosomes (Fig. 2i).

Pardosa bifasciata (C.L. Koch 1834)

The male karyotype is comprised of 28 acrocentric chromosomes, including two X chromosomes (Fig. 2j). Autosomes gradually decrease in size (Fig. 1d). The relative length of first autosomal pair was 8.63 and the last was 5.09% (Table 2). Relative lengths of sex chromosomes were 7.64 and 6.24%. During pachytene, X_1 and X_2 were tightly aligned forming so-called sex vesicle (Fig. 2k). At diakinesis, there were 13 autosomal bivalents, two positively heteropycnotic univalents the sex chromosomes (Fig. 2l).

Arctosa cinerea (Fabricius 1777)

The karyotype of *A. cinerea* possessed 28 chromosomes, including two X chromosomes (Fig. 2m). All autosomal pairs were acrocentric

Table 1.—Karyotype characteristics, collecting locality and geographical coordinates of the five Gnaphosidae and Lycosidae species cytogenetically analyzed.

Species	2n ♂	n ♂	Sex/stage	Locality and coordinates
Gnaphosidae				
Nomisia conigera	22	10 + XX	3 ♂ (1 subadult, 2 adults), 07 March 2009	Gaziantep/ Sakçagözü 37°11′N, 36°58′E
			1♂ (1 adult), 22 March 2009	Kırşehir/ Çiçekdağ 39°36′N, 34°24′E
			7 ♂ (2 subadults, 5 adults) 28 March 2009, 04 April 2009	Gaziantep/ Nurdağı 37°10′N, 36°44′E
Haplodrassus morosus	22	10 + XX	4 ♂ (adults), 04 April 2009	Gaziantep/ Islahiye 37°01′N, 36°37′E
			2 ♂ (adults), 04 April 2009	Hatay/ Altınözü 36°13′N, 36°09′E
			3 ♂ (1 subadult, 2 adults) 18 April 2009	K.Maraş/ Pazarcık 37°29′N, 37°17′E
Haplodrassus dalmatensis	22	10 + XX	2 ♂ (1 subadult, 1 adult) 14 March 2009	Osmaniye/ Merkez 37°03′N, 36°16′E
			3 ♂ (adult), 25 April 2009	Adıyaman/ Kahta 37°48′N, 38°36′E
			2 ♂ (2 adults), 02 May 2009	Gaziantep/ Merkez 37°06′N, 37°18′E
Lycosidae				
Pardosa bifasciata	28	13 + XX	8 ♂ (2 subadults, 6 adults), 07 March 2009, 28 March 2009, 04 April 2009	Gaziantep/ Nurdağı 37°10′N, 36°42′E
			1♂ (1 adult), 21 March 2009	Kırşehir/ Mucur 39°04′N, 34°22′E
			2♂ (2 adults), 11 April 2009	Adıyaman / Sincik 38°03′N, 38°38′E
			2♂ (2 adults), 18 April 2009	Gaziantep/ Araban 37°24′N, 37°41′E
Arctosa cinerea	28	13 + XX	5♂ (1 subadult, 4 adults) 11April 2009	Adıyaman/ Kahta 37°46′N, 38°38′E
			2♂ (2 adults), 11April 2009	Adıyaman/ Sincik 38°02′N, 38°36′E

and gradually decreased in size (Fig. 1e). In the spermatogonial metaphase, the length of autosome pairs change from 4.85 to 8.26%. Relative lengths of sex chromosomes X_1 and X_2 were 7.38 and 5.73%, respectively. During the first stages of prophase I, X_1 and X_2 were positively heteropycnotic. At the diplotene stage, we observed 13 autosomal bivalents and two univalents (Fig. 2n). Two types of anaphase I plates were found with 13 and 15 chromosomes (Fig. 2o).

DISCUSSION

Cytogenetic studies on the majority of gnaphosid and lycosid spiders reveal similar characteristics: acrocentric or telocentric chromosomes, sex chromosome system in male/female, $X_1X_2♂$/ $X_1X_1X_2X_2♀$, and chiasmatic meiosis. Chromosomes with metacentric and submetacentric morphology and sex chromosome system of the type X and $X_1X_2X_3$ in males are uncommon (Kumbıçak et al. 2009).

Until now, only one species belonging to the genus *Nomisia* has been studied cytogenetically. *N. riparensis* (O. Pickard-Cambridge 1872) was shown to have 2n = 22 in males and 2n = 24 in females with a X_1X_2 type of sex chromosome system (Table 3). Male *N. conigera* show a diploid chromosome number of 2n = 22 and a X_1X_2 type of sex determining system. Therefore, our results are similar to the *N. riparensis* previously studied (Table 3). The gnaphosid *N. conigera* has significantly different relative lengths of X_1 and X_2. The gnaphosid genera *Callilepis* (Westring 1874) and *Drassodes* (Westring 1851) exhibited dissimilar characteristics in sex chromosomes. In addition, sex chromosomes are the largest elements of *N. conigera* but not of *Callilepis* and *Drassodes* (Painter 1914; Hackman 1948; Suzuki 1954).

The 2n = 22, X_1X_2, acrocentric chromosomes were also described by Hackman (1948) and Gorlov et al. (1997) in *Haplodrassus cognatus* (Westring 1861) and *Haplodrassus signifer* (C.L. Koch 1839), respectively (Table 3). *Haplodrassus morosus* and *H. dalmatensis* have the same diploid number and also the same sex chromosome system. This result, coupled with existing data, supports the hypotheses of a relatively conserved diploid number and sex chromosome system in the family Gnaphosidae. Our results on *H. morosus* and *H. dalmatensis* reveal that there is no significant difference in the relative length of X_1 and X_2 (Table 2).

Ten species of *Arctosa* (C.L. Koch 1847) have been studied so far. With the exception of the results by Akan *et al.* (2005), the diploid chromosome number is 2n = 26 or 28 and the sex chromosome system in males is a X_1X_2 type. The results provided by Akan *et al.* (2005) for *Arctosa perita* (Latreille 1799) were problematic and the reported diploid chromosome number for females (2n = 12) was improbable as the lowest diploid number (Dolejš 2011). The diploid chromosome number and sex chromosome system was determined as 2n = 28 and X_1X_2 for *Arctosa cinerea* (Fabricius 1777) by Dolejš *et al.* (2011), and our karyotype results for *A. cinerea* show similar characteristics (Table 3). Up to now, 25 species belonging to the genus *Pardosa* (C.L. Koch 1847) have been investigated cytogenetically. Most of them have 2n = 28 in males and 2n = 30 in females, but *Pardosa basiri* (Dyal 1935) was found to have 2n♂ = 22, *Pardosa leucopalpis* (Gravely 1924) and *Pardosa sumatrana* (Thorell 1890) 2n♂ = 24 and *Pardosa oakleyi* (Gravely 1924) 2n♂ = 26 (Kumbıçak et al. 2009). Male *P. bifasciata* shows a diploid chromosome number of 2n = 28. Like the previously studied species of *Pardosa*, the sex chromosome system for *P. bifasciata* is a X_1X_2 type (Table 3).

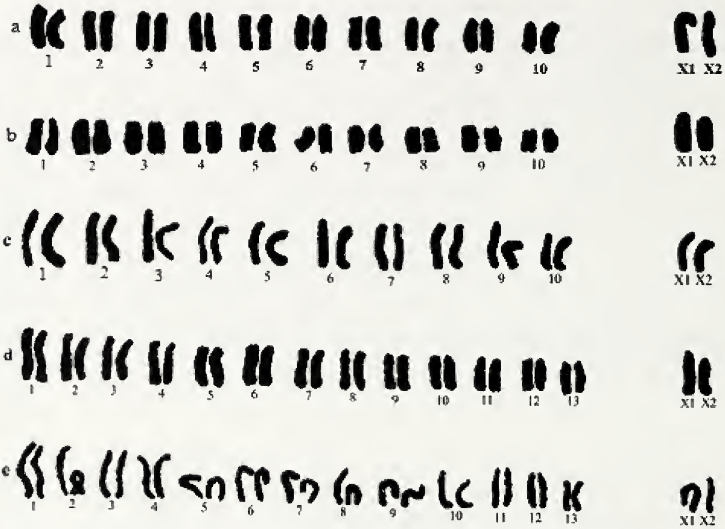


Figure 1.—Karyotypes of gnaphosid and lycosid species analyzed in this study. a. *Nomisia conigera*, b. *Haplodrassus morosus*, c. *Haplodrassus dalmatensis*, d. *Pardosa bifasciata*, e. *Arctosa cinerea* (Bar = 10 μm).

ACKNOWLEDGMENTS

We wish to thank Dr. Osman Seyyar for spider determination. Also, we would like to express our thanks to Abdullah Doğan, who kindly helped in field studies.

LITERATURE CITED

Akan, Z., I.M. Varol & M. Özaslan. 2005. A cytotaxonomical investigation on spiders (Arachnida: Araneae). Biotechnology and Biotechnological Equipment 19:101–104.

Bernard, C.J. 2005. Meiosis (Developmental and Cell Biology Series). Cambridge University Press, Cambridge, UK.

Bole-Gowda, B.N. 1958. A study of the chromosomes during meiosis in twenty-two species of Indian spiders. Proceeding of the Zoological Society of Bengal 11:69–108.

Chemisquy, M.A., S.G.R. Gil, C.L. Scioscia & L.M. Mola. 2008. Cytogenetic studies of three Lycosidae species from Argentina (Arachnida, Araneae). Genetics and Molecular Biology 31:857–867.

Dolejš, P., T. Kořínková, J. Musilová, V. Opatová, L. Kubková, J. Buchar & J. Král. 2011. Karyotypes of Central European spiders of the genera *Arctosa*, *Tricca* and *Xerolycosa* (Araneae:Lycosidae). European Journal of Entomology 108:1–16.

Gorlov, I.P., O.Y. Gorlova & D.V. Logunov. 1995. Cytogenetic studies on Siberian spiders. Hereditas 122:211–220.

Gorlova, O.Y., I.P. Gorlov, E. Nevo & D.V. Logunov. 1997. Cytogenetic studies on seventeen spider species from Israel. Bulletin of the British Arachnological Society 18:249–252.

Hackman, W. 1948. Chromosomenstudien an Araneen mit besonderer Berücksichtigung der Geschlechtschromosomen. Acta Zoologica Fennica 54:1–101.

Kageyama, A., T. Seto & H. Inoue. 1978. Chromosomes of Japanese lycosid spiders. Chromosome Information Service 25:26–27.

Kumbýçak, Z., S. Ergene & S. Saygıdeğer. 2009. Chromosomal data of six araneomorph spiders belonging to the families Lycosidae and Gnaphosidae (Araneae: Araneomorphae). Zoology in the Middle East 48:89–96.

Mittal, O.P. 1960. Chromosome number and sex mechanism in twenty species of the Indian spiders. Research Bulletin of Panjab University Science 11:245–247.

Mittal, O.P. 1963. Karyological studies on the Indian spiders. I. A comparative study of the chromosomes and sex determinating mechanism in the family Lycosidae. Research Bulletin of Panjab University Science 14:59–86.

Painter, T.S. 1914. Spermatogenesis in spiders. Zoologisches Jahrbuch, Abteilung Anatomie und Ontogenie der Tiere 38:509–576.

Sharma, G.P., M.S. Jande, M.S. Grewal & R.N. Chorpa. 1958. Cytological studies on the Indian spiders. II. Chromosome complement and male meiosis in seven species of the family Lycosidae. Research Bulletin of Panjab University 156:255–269.

Sharma, G.P. 1961. A study on the chromosomes of two lycosid spiders. Proceedings Zoological Society Calcutta 14:33–38.

Sharma, G.P. & B.L. Gupta. 1956. Cytological studies on the male germ cells of the spider, *Pardosa* sp., with observations under the phase contrast microscope. Research Bulletin of Panjab University Science 84:5–19.

Srivastava, M.D.L. & S. Shukla. 1986. Chromosome number and sex-determining mechanism in forty-seven species of Indian spiders. Chromosome Information Service 41:23–26.

Suzuki, S. 1954. Cytological studies in spiders. III. Studies on the chromosomes of fifty-seven species of spiders belonging to seventeen families, with general considerations on chromosomal evolution. Journal of Science of Hiroshima University 15:23–136.

Traut, W. 1976. Pachytene mapping in the female silkworm *Bombyx mori* L. (Lepidoptera) Chromosoma 58:275–284.

Manuscript received 26 January 2011, revised 27 September 2011.

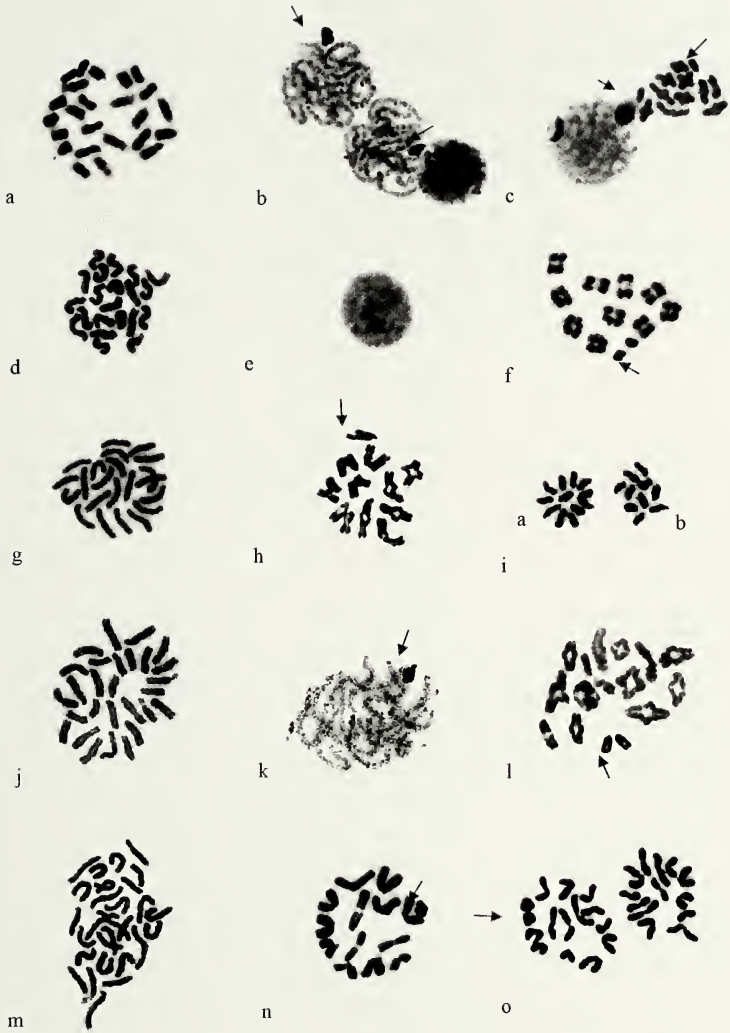


Figure 2.—*Nonisia conigera* a. Spermatogonial metaphase 2n = 22. b. Pacytene nucleus with positively heteropycnotic sex chromosomes (arrows). c. Diplotene with 13 autosomal bivalents and two sex chromosomes (arrows); *Haplodrassus morosus*. d. Spermatogonial metaphase 2n = 22. e. Leptotene nucleus with isopycnotic sex chromosomes. f. First meiotic division metaphase plate with two sex chromosomes (arrow); *Haplodrassus dalmatensis*. g. Spermatogonial metaphase 2n = 22. h. Diplotene with 10 autosomal bivalents and two univalent sex chromosomes (arrow). i. Second meiotic division anaphase plate with 12 (a) and 10 (b) chromosomes; *Pardosa bifasciata*. j. Spermatogonial metaphase 2n = 28. k. Pacytene nucleus with positively heteropycnotic sex vesicle (arrow). l. Diakinesis with 13 autosomal bivalents and two sex chromosomes (arrow); *Arctosa cinerea*. m. Spermatogonial metaphase 2n = 28. n. Diplotene with 13 autosomal bivalents and two associated sex chromosomes (arrow). o. First meiotic division anaphase plate with two sex chromosomes (arrow). (Bar = 10 μm).

Table 2.—Relative length of particular chromosome pairs (RCL) and centromeric indexes (CI) of species studied. Based on spermatogonial metaphases.

	Nomisia conigera		*Haplodrassus morosus*		*Haplodrassus dalmatensis*		*Pardosa bifasciata*		*Arctosa cinerea*	
Pair No	RCL	CI	RCL	CI	RCL	CI	RCL	CI	RCL	CI
1	10.15	10.49	11.47	13.80	10.28	8.09	8.63	7.39	8.26	7.72
2	10.12	8.63	9.06	12.05	9.65	7.42	7.82	7.35	7.75	7.02
3	8.50	7.53	8.61	7.28	9.64	9.71	7.39	13.02	7.46	12.00
4	8.34	9.12	8.46	8.29	9.33	7.38	7.30	7.48	7.35	18.00
5	7.99	9.43	8.14	7.71	8.37	10.81	6.92	9.71	7.26	8.50
6	7.94	19.33	7.99	7.73	8.36	7.64	6.91	20.87	7.16	11.66
7	6.53	9.76	7.84	9.65	8.36	17.05	6.86	9.4	6.76	13.46
8	6.03	9.17	7.23	8.40	7.72	8.67	6.66	9.74	6.57	7.96
9	5.77	12.75	6.31	9.25	7.39	8.50	6.54	18.11	6.50	22.86
10	5.38	10.62	5.99	12.00	6.92	9.43	5.41	7.2	5.93	7.51
11							5.31	18.19	5.84	22.57
12							5.28	13.81	5.20	10.63
13							5.09	13.88	4.85	20.78
X_1	13.01	8.01	10.29	10.16	7.55	8.4	7.64	10.6	7.38	13.03

Table 3.—List of karyotyped species of the genera *Pardosa* and *Arctosa* (Lycosidae) and genera *Nomisia* and *Haplodrassus* (Gnaphosidae). Abbreviations: NMC: Number and morphology of chromosomes in male, SCS: Sex chromosome system, a: acrocentric.

Family/Species	NMC	SCS	References
Lycosidae			
Arctosa alpigena (Doleschall 1852)	26; a	X_1X_2	Hackman 1948
Arctosa leopardus (Sundevall 1833)	26; a	X_1X_2	Hackman 1948
Arctosa sp.	28; a	X_1X_2	Mittal 1960, 1963
Arctosa mulaii (Dyal 1935)	28; a	X_1X_2	Sharma et al. 1958
Arctosa alpigena lamperti (Dahl 1908)	28; a	X_1X_2	Dolejš et al. 2011
Arctosa cinerea (Fabricius 1777)	28; a	X_1X_2	Dolejš et al. 2011
Arctosa figurata (Simon 1876)	28; a	X_1X_2	Dolejš et al. 2011
Arctosa maculata (Hahn 1822)	28; a	X_1X_2	Dolejš et al. 2011
Arctosa perita (Latreille 1799)	28; a	X_1X_2	Dolejš et al. 2011
Arctosa renidescens Buchar &Thaler 1995	28; a	X_1X_2	Dolejš et al. 2011
Pardosa agrestis (Westring 1861)	28; a	X_1X_2	Gorlov et al. 1995
Pardosa agricola (Thorell 1856)	28; a	X_1X_2	Hackman 1948
Pardosa amentata (Clerck 1757)	28; a	X_1X_2	Hackman 1948
Pardosa astrigera (L. Koch 1878)	28; a	X_1X_2	Suzuki 1954
Pardosa basiri (Dyal 1935)	22; a	X_1X_2	Mittal 1960, 1963
Pardosa birmanica Simon 1884	28; a	X_1X_2	Bole-Gowda 1958
Pardosa fletcheri (Gravely 1924)	28; a	X_1X_2	Srivastava & Shukla 1986
Pardosa lahorensis Dyal 1935	28; a	X_1X_2	Sharma et al. 1958
Pardosa laura Karsch 1879	28; a	X_1X_2	Kageyama et al.1978
Pardosa leucopalpis Gravely 1924	28; a	X_1X_2	Bole-Gowda 1958
Pardosa leucopalpis Gravely 1924	24; a	X_1X_2	Srivastava & Shukla 1986
Pardosa lugubris (Walckenaer 1802)	28; a	X_1X_2	Gorlov et al. 1995
Pardosa monticola (Clerck 1757)	28; a	X_1X_2	Hackman 1948
Pardosa oakleyi Gravely 1924	26; a	X_1X_2	Srivastava & Shukla 1986
Pardosa palustris (Linnaeus 1758)	28; a	X_1X_2	Hackman 1948
Pardosa pseudoannulata (Bösenberg & Strand 1906)	28; a	X_1X_2	Suzuki 1954
Pardosa pullata (Clerck 1757)	28; a	X_1X_2	Hackman 1948
Pardosa sumatrana (Thorell 1890)	24; a	X_1X_2	Sharma 1961
Pardosa plumipes (Thorell 1875)	28; a	X_1X_2	Gorlov et al. 1995
Pardosa alacris (C.L. Koch 1833)	28; a	X_1X_2	Kumbıçak et al. 2009
Pardosa saltans (Töpfer-Hofman 2000)	28; a	X_1X_2	Kumbıçak et al. 2009
Pardosa sp. 1	28; a	X_1X_2	Bole-Gowda 1953, 1958
Pardosa sp. 2	28; a	X_1X_2	Sharma and Gupta 1956
Pardosa sp. 3	28; a	X_1X_2	Mittal 1960
Gnaphosidae			
Nomisia riparienisis (O. Pickard-Cambridge 1872)	22; a	X_1X_2	Gorlova et al. 1997
Haplodrassus cognatus (Westring 1861)	22; a	X_1X_2	Hackman 1948
Haplodrassus signifer (C.L. Koch 1839)	22; a	X_1X_2	Gorlova et al. 1997

2011. The Journal of Arachnology 39:495–496

SHORT COMMUNICATION

Egg hiding in four harvestman species from Uruguay (Opiliones: Gonyleptidae)

Estefanía Stanley: Laboratorio de Etología, Ecología y Evolución, Instituto de Investigaciones Biológicas Clemente Estable, Avenida Italia 3318, CP 11600, Montevideo, Uruguay. E-mail: estefaniastanley@gmail.com

Abstract. I describe oviposition sites and egg-hiding for four species of the family Gonyleptidae: *Parampheres bimaculatus*, *Parampheres ronae* (Gonyleptinae), *Discocyrtus prospicuus*, and *Pachyloides thorellii* (Pachylinae). Females of *P. bimaculatus* bury single eggs on the ground; the first record of this behavior among gonyleptids. Females of the other three species lay their eggs, singly or in clusters, on tree trunks or rock fissures. I found the eggs of *P. ronae* and *D. prospicuus* covered with debris, whereas eggs of *P. thorellii* were not. Females of *D. prospicuus* and *P. thorellii* lay their eggs over an extended period of time. At least for hemipterans, covering the eggs with debris works as a way to camouflage or prevent egg dehydration. I hypothesize that for the species used in this study, to spread isolated eggs in time and space may also protect them against predators and parasites.

Keywords: *Discocyrtus*, *Parampheres*, *Pachyloides*, egg burying, oviposition, parental care

Many cases of post-ovipositional maternal care and post-ovipositional paternal care have been described for representatives of the Neotropical Gonyleptidae in the last two decades (Machado & Macías-Ordóñez 2007). Although egg-hiding is regarded as the most common form of parental care in the family (Machado & Raimundo 2001), there are few descriptions of this behavior in the arachnological literature. In this study, I describe oviposition sites and egg-hiding for four species of the family Gonyleptidae without post-ovipositional parental care. Reproductive behavior of two species, *Parampheres bimaculatus* (Mello-Leitão 1932) and *P. ronae* (Mello-Leitão 1927) (Gonyleptinae), previously undescribed, and reproductive behavior of the remaining two, *Discocyrtus prospicuus* (Holmberg 1876) and *Pachyloides thorellii* (Holmberg 1878) (Pachylinae), has only been briefly mentioned by Canals (1936).

All species were collected during February 2009. *Parampheres bimaculatus, D. prospicuus*, and *P. thorellii* were collected in two localities, Marindia (34°46′S, 55°49′W) and Piedras de Afilar (34°45′S, 55°33′W), both in the Department of Canelones; *P. ronae* was collected in Cerro Verde (33°56′S, 56°30′W) in the Department of Rocha, eastern Uruguay. I found the individuals during daylight, under rocks and rotten trunks located in grassland landscapes. I placed collected animals in four different terraria (40 × 20 cm base, 20 cm height), one for each species (13 *P. bimaculatus* (9 female, 4 male), 12 *P. ronae* (9 female, 3 male), 15 *D. prospicuus* (10 female, 5 male), and 17 *P. thorellii* (10 female, 7 male)). All terraria contained sand and soil as substrate, cotton embedded with water as a water source, and rocks and pieces of wood to provide a variety of refuges for the individuals. All the individuals were fed pieces of larvae of *Tenebrio mollitor* (Coleoptera, Tenebrionidae), dead adults of *Acheta domesticus* (Orthoptera, Gryllidae), apple and cucumber, once a week. Behavioral data were based on daily opportunistic observations made during the afternoon (15:00–18:00 h) in June 2009 at room temperature (15.0 ± 1.6° C, mean ± SD) under natural light. Voucher specimens were housed in the Colección Entomológica of the Facultad de Ciencias, Montevideo, Uruguay.

I observed one *P. bimaculatus* female oviposit three times on the same day. First, the female walked around touching the substrate with the tarsus of her first pair of legs and stopped at an isolated place. Standing on that place, she repeatedly touched a point in the substrate with the dorsal part of the tarsi of the first pair of legs, and occasionally with the same part of the metatarsi of the same pair of legs. Through these movements with the first pair of legs, which lasted ~ 4 min, the female dug a small hole on the ground (ca 0.5 cm diam.). Next, she remained quiescent for approximately 5 min, and then everted her ovipositor. In this position, the female touched the ovipositor using the first pair of legs for nearly 3 min before laying an egg inside the hole in the ground. Finally, remaining still on that place, the female used her first pair of legs to drag little pieces of wood and other particles of the substrate towards the egg until it was completely buried (this behavior lasted ~ 7 min), and then she abandoned the oviposition site. This same female walked around for nearly 5 min and resumed the same behavioral sequence described above, which ended with another egg buried in the ground 5 cm from the first egg. Five minutes later, a third egg was laid 5 cm from the second one and the oviposition behavior followed the same general pattern described for the first egg. The female did not coat any of the eggs with mucus. I recorded one egg cannibalism event in this species: an adult male dug up and ate one of the eggs laid earlier that day.

During the observation periods, two *P. ronae* females laid one egg each inside fissures of a piece of wood. Both observations started when I noticed the females with the everted ovipositor having an egg on its apex. Ovipositing females remained in this position for ~ 3 min and then lowered the anterior region of the body, depositing the egg inside the fissure. In the sequence, females retracted the ovipositor and used mostly the second (but also the first pair of legs) to cover the eggs with debris, such as sand grains and particles of dust, wood, or soil. During the egg-covering process, females scraped the substrate around the fissure, picked up debris, and gently attached particles to the egg surface. They did not coat the egg with mucus, as described for other gonyleptid species (Machado et al. 2004). Once each female covered the egg completely, she left the oviposition site. In addition to these two oviposition events for this species, I found in the terraria both isolated eggs ($n = 8$) and small clusters ($n = 2$) of up to six eggs on pieces of wood, all of them covered with debris.

For *D. prospicuus* ($n = 6$) and *P. thorellii* ($n = 30$), I did not observe oviposition behavior, but I found eggs inside the terraria. No *D. prospicuus* egg was coated with mucus, but I found all of them covered with debris. I located five individual eggs each inside rock fissures and one small cluster of five eggs spaced out by 0–1 cm on the bottom of a piece of wood. Females of *P. thorellii* always laid isolated eggs on the wet cotton wool ($n = 20$), inside fissures in pieces of wood ($n = 7$), or under rocks ($n = 3$). In contrast to Canals's (1936) observations, I never found eggs of this species covered with debris.

Egg-burying described for *P. bimaculatus* females probably represents the first record of this behavior in the family Gonyleptidae. Although eggs buried in the ground are more likely to be protected

from predators than eggs laid on exposed surfaces, a cannibalism event by an adult male was registered. Observations in nature are necessary to confirm this behavior as it is based in only one event.

The oviposition behavior I describe for *P. ronae* is similar to other Gonyleptinae species that do not engage in parental care, such as *Mischonyx cuspidatus*, the females of which lay isolated eggs on the soil and under fallen trunks (Pereira et al. 2004). To cover the eggs with debris, however, seems to be a widespread behavior within this subfamily because it is observed even in species with post-ovipositional paternal care, such as *Gonyleptes saprophilus* and *Neosadocus* sp. (Machado et al. 2004).

Among the subfamily Pachylinae, which comprises nearly 400 species (Kury 2003), there are records of post-ovipositional maternal care and egg-hiding. Post-ovipositional maternal care in the group is always associated with clustered oviposition, whereas egg-hiding is always associated with oviposition of isolated eggs (Machado & Raimundo 2001). Independent of the form of parental care, most pachyline species cover the eggs with debris, which is generally interpreted as a way to camouflage or prevent egg dehydration (Willemart 2001; Elpino-Campos et al. 2001). However, as described in this study, *P. thorellii* does not cover the eggs. This species inhabits extremely humid places where there almost no light or air currents exist; such habitat conditions are different from those of the other species studied here. Therefore, future studies should focus on evaluating these differences in order to find the possible cause of *P. thorelliis*'s unique behavior among members of its subfamily.

At least for hemipterans, the act of hiding eggs by depositing them either at varying times or in different locations is probably as efficient as post ovipositional maternal care in ensuring that the eggs are protected against predators and parasites (Tallamy & Schaefer 1997). Since individuals of both *D. prospicuus* and *P. thorellii* can be found living syntopically with individuals of *Acanthopachylus aculeatus*, the females of which exhibit post-ovipositional maternal care (Capocasale & Bruno-Trezza 1964; Toscano-Gadea 2008), it would be interesting to compare offspring survival in these species to test the efficiency of different forms of parental care in harvestmen.

I thank Carlos A. Toscano-Gadea for helping me take care of the individuals, for the constant support, and for the useful comments and suggestions on this work. I would also like to thank Anita Aisenberg for critically reading the manuscript. Finally, I would like to thank both reviewers whose comments significantly improved this work.

LITERATURE CITED

Canals, J. 1936. Observaciones biológicas en arácnidos del orden Opiliones. Revista Chilena de Historia Natural 40:61–63.

Capocasale, R. & L.B. Bruno-Trezza. 1964. Biología de *Acanthopachylus aculeatus* (Kirby, 1819), (Opiliones: Pachylinae). Revista de la Sociedad Uruguaya de Entomología 6:19–32.

Elpino-Campos, A., W. Pereira, K. Del-Claro & G. Machado. 2001. Behavioral repertory and notes on natural history of the Neotropical harvestman *Discocyrtus olivierioi* (Opiliones: Gonyleptidae). Bulletin of the British Arachnological Society 12:144–150.

Kury, A.B. 2003. Annotated catalogue of the Laniatores of the New World (Arachnida, Opiliones). Revista Ibérica de Aracnología, volumen especial monográfico 1:1–337.

Machado, G. & R. Macías-Ordóñez. 2007. Reproduction. Pp. 414–454. *In* Harvestmen: the Biology of Opiliones. (R. Pinto da Rocha, G. Machado & G. Giribet, eds.). Harvard University Press, Cambridge, Massachusetts.

Machado, G. & R.L.G. Raimundo. 2001. Parental investment and the evolution of subsocial behaviour in harvestmen (Arachnida: Opiliones). Ethology Ecology and Evolution 13:133–150.

Machado, G., G.S. Requena, B.A. Buzatto, F. Osses & L.M. Rossetto. 2004. Five new cases of paternal care in harvestmen (Arachnida: Opiliones): implications for the evolution of male guarding in the Neotropical family Gonyleptidae. Sociobiology 44:577–598.

Pereira, W., A. Elpino-Campos, K. Del-Claro & G. Machado. 2004. Behavioral repertory of the Neotropical harvestman *Ilhaia cuspidata* (Opiliones, Gonyleptidae). Journal of Arachnology 32:22–30.

Tallamy, D.W. & C. Schaefer. 1997. Maternal care in the Hemiptera: ancestry, alternatives, and current adaptive value. Pp. 94–115. *In* The Evolution of Social Behavior in Insects and Arachnids. (J.C. Choe & B.J. Crespi, eds.). Cambridge University Press, Cambridge, UK.

Toscano-Gadea, C.A. 2008. Descripción del cuidado maternal en *Acanthopachylus aculeatus* (Opiliones, Gonyleptidae). Libro de resúmenes del Segundo Congreso Latinoamericano de Aracnología.

Willemart, R.H. 2001. Egg covering behavior of the Neotropical harvestman *Promitobates ornatus* (Opiliones, Gonyleptidae). Journal of Arachnology 29:249–252.

Manuscript received 31 December 2010, revised 26 April 2011.

2011. The Journal of Arachnology 39:497–499

SHORT COMMUNICATION

Paternal care in a Neotropical harvestman (Opiliones: Cosmetidae) from Costa Rica

Daniel N. Proud: Department of Biology, University of Louisiana at Lafayette, Lafayette, Louisiana 70504-2451 USA

Carlos Víquez: INBio, Apdo. 22-3100, Santo Domingo, Heredia, Costa Rica

Victor R. Townsend, Jr.[1]: Department of Biology, Virginia Wesleyan College, 1584 Wesleyan Drive, Norfolk, Virginia 23502 USA

Abstract. Although relatively rare among harvestmen in the superfamily Gonyleptoidea, paternal care has been observed in the families Manaosbiidae and Gonyleptidae, but not previously in the Cosmetidae. In this study, we describe multiple observations of egg guarding by adult males of an undescribed species of cosmetid harvestman from Volcán Cacao, Guanacaste Province, Costa Rica. Observations were made from 26–28 July 2010, during the wet season. In this species, males only guard eggs after dusk, leaving eggs unattended during the day. Based upon differences in color and size, males guarded eggs through several stages of development. When guarding, males contacted the first two pairs of legs with the eggs. Oviposition sites consisted of the undersides of leaves of small plants, with eggs closely packed together in a single layer covered by abundant, transparent mucus. The largest, darkest eggs were located near the distal tip of the leaf.

Keywords: Behavioral ecology, Central America, egg guarding, polyandry, reproduction

In this study, we describe multiple observations of egg guarding by adult males of an undescribed species of cosmetid harvestman in Central America. Among Neotropical harvestmen of the suborder Laniatores, parental care may take several forms including the guarding of nymphs and the burying, hiding, carrying, or guarding of eggs (Machado & Raimundo 2001) and is performed by the adult female or male (Machado & Macías-Ordóñez 2007). Maternal care, though generally more common, is restricted to the Gonyleptoidea, including species in the families Cosmetidae (Goodnight & Goodnight 1976), Cranaidae (Machado & Warfel 2006; Hunter et al. 2007), Gonyleptidae (Machado & Raimundo 2001) and Stygnopsidae (Mitchell 1971). In contrast, exclusive paternal care is relatively rare and is known to occur in species from the families Assamiidae (Martens 1993), Gonyleptidae (Hara et al. 2003; Machado et al. 2004), Manaosbiidae (Rodríguez & Guerrero 1976; Mora 1990), Podoctidae (Martens 1993) and Triaenonychidae (Forster 1954, but see Machado 2007). True biparental care of eggs or nymphs has not been conclusively demonstrated. However, in *Goniosoma longipes* (Gonyleptidae), males will assume parental care if the guarding female is removed (Machado & Oliveira 1998).

In general, there are considerable, consistent differences between the sexes with respect to egg guarding behavior. In the field, maternal care is essential for preventing egg predation by insects, including ants (Machado & Oliveira 2002) and crickets (Machado & Oliveira 1998). In the manaosbiid harvestman *Zygopachylus albomarginis*, adult males effectively protect eggs against fungal growth and cannibalism by conspecifics (Mora 1990). The guarding of eggs by male harvestmen may also attract females, enabling these individuals to mate more frequently than conspecifics that are not associated with eggs (Nazareth & Machado 2010). In species with maternal care, females generally only guard eggs of the same age (same stage of development), and the eggs are guarded continuously (Machado & Macías-Ordóñez 2007). In contrast, males often guard eggs of different ages (multiple stages of development) and may regularly leave the eggs to undertake other activities, such as foraging (Hara et al. 2003; Machado et al. 2004).

[1] Corresponding author. Email: vtownsend@vwc.edu

We observed cosmetid harvestmen in the field from 26–28 July 2010 at Cacao Field Station (10°55′15.79″N, 85°28′3.53″W, elev. 1049 m) on the southwestern slope of Guanacaste National Park, Guanacaste Province, Costa Rica. The forested habitat in this area features a canopy height of approximately 20 m with an understory composed of small plants, generally less than 0.5 m in total height. During evening observations (2100–2300 h), air temperature was approximately 20–21° C and relative humidity was nearly 99%, with little to no wind or rain.

Over the three-day period, we observed four instances of paternal care. Egg batches (A, B, C and D) were observed for 15-min periods each, at approximately 12 and 24 h increments following their discovery. All eggs were covered in a thick, transparent mucus coat (Fig. 1A, B). Egg batches A, C and D occurred on the underside of leaves of the same species of small unidentified plant (Sapotaceae), while egg batch B (Fig. 1B) was on the underside of a leaf of *Symphonia globulifera* (Clusiaceae). On 26 July 2010 at 2100 h, we located egg batches A and B on the underside of leaves from plants that were 30 cm tall. The plants were no more than 2 m apart and the eggs and guarding males were on the undersides of leaves, approximately 10 cm above the ground (Fig. 1A). When initially disturbed, the adult males actively waved legs I and II over the eggs and occasionally touched them, most frequently with leg I. Egg batch A contained 39 eggs at two different stages of development (based on egg color and size). Egg batch B had approximately 150 eggs representing at least two different stages of development. We photographed the egg batches and marked their location with flagging. At 0800 h the following day, we relocated the unattended egg batches. We briefly searched the surrounding leaf litter and adjacent plants, but did not find either male. Later that evening (27 July) at 2100 h, we returned and found that both males had resumed guarding their eggs. We observed the males, collected the leaf containing the eggs and male, placed them into the same container and monitored them for 72 h. Males continued guarding eggs, but no hatching occurred over this interval, so we preserved the eggs and the males in 70% ethanol.

During the evening of 27 July, we discovered two additional egg batches, approximately 10 m from the first two batches. Egg batch C was 5 cm above the ground on the underside of a leaf and contained

Figure 1.—Paternal care by an undescribed species of cosmetid harvestman. A. Male guarding an egg batch on the underside of a leaf (Sapotaceae) that is approximately 10 cm above the litter. B. Egg batch with eggs at two developmental stages on the distal tip of leaf of *Symphonia globulifera* (Clusiaceae). The eggs are covered in a thick mucus coat, and those closest to the leaf margin are darker and seem to have been laid first.

17 eggs at two different stages of development. When disturbed, the guarding male actively waved legs I and II over the eggs. Egg batch D was approximately 4 m away from batch C and was 10 cm above the ground. This batch had 57 eggs at two different stages of development. We observed and photographed the batches and marked their locations with flagging. At 0800 h on the following day, we returned and found the eggs unguarded. We did not collect these eggs.

Our natural history observations offer new and important insights into the reproductive biology of Laniatores harvestmen and the evolution of paternal care. The ovipositional pattern and paternal care that we observed has previously only been reported for species from the sister subfamilies Caelopyginae and Progonyleptoidellinae of the Gonyleptidae (Machado et al. 2004). In these gonyleptid harvestmen, eggs are 1) deposited on the undersurface of leaves; 2) laid from the apex to the base of the leaf; 3) covered in a thick mucus coat and 4) guarded by males during postzygotic development. Cosmetid harvestmen are not phylogenetically closely related to this group; thus, our observations represent the first report of a new, independent event in the evolution of paternal care in harvestmen.

In several gonyleptid harvestmen that exhibit paternal care, sexual dimorphism with respect to body size and the armature of leg IV is generally reduced (Kury & Pinto-da-Rocha 1997; Pinto-da-Rocha 2002). However, in other species with paternal care, strong sexual dimorphism is associated with defense by the male of a specific and scarce resource, such as a tree hole (Machado et al. 2004; Nazareth & Machado 2009). In the cosmetid species that we examined there was little sexual dimorphism with respect to body size or the armature of leg IV. However, this species is unique among the 133 formally described cosmetid species from Central America (Townsend et al. 2010), because males only have four tarsomeres on leg I, whereas females have five. In addition, the two most basal tarsal segments on leg I are enlarged in the male, but not in the female. Given that sexual differences in the relative size of the basal tarsomeres are very common among cosmetid harvestmen, it seems likely that this dimorphism reflects sexual selection for intra- or intersexual communication, rather than egg guarding.

Our observations represent important contributions to the natural history of harvestmen in the family Cosmetidae, the second largest group of Neotropical (> 700 described species) harvestmen. Little is known about the fecundity, frequeney of reproduction, parental care, or preferences for oviposition sites of most species (Machado & Macías-Ordóñez 2007). In two Nearctie cosmetid species of *Vonones,* females produce a single batch of 85 or more eggs and cover or hide them (Goodnight 1958; Cokendolpher & Jones 1991). Oviposition sites include fallen tree trunks, leaf litter and the inside crevices of moist wood (Machado & Macías-Ordóñez 2007). In other Neotropical cosmetid species from the Caribbean and South America, females lay one or two batches of 90–240 eggs and generally cover and hide their eggs (Canals 1936; Juberthie 1972; Friebe & Adis 1983). The only cosmetid harvestman from Central America that has been studied is *Erginulus clavotibialis* (Goodnight & Goodnight 1976). In this species females produce a single batch of 90–100 eggs, with oviposition occurring in spaces under tree bark or in crevices. In contrast to other cosmetid species, however, female *E. clavotibialis* actively guard their eggs.

During our field observations we observed that egg batches were only guarded by males at night, and that each batch contained eggs at different stages of development. These behavioral patterns are similar to those observed in other Neotropical harvestmen (Hara et al. 2003; Machado et al. 2004). In the manaosbiid *Zygopachylus albomarginis* (Mora 1990) and the gonyleptid *Iporangaia pustulosa* (Machado et al. 2004), rival males consume unprotected eggs. Machado et al. (2004) provided three possible explanations for why male parental care is discontinuous, including the hypotheses that 1) males lack sufficient energy reserves to sustain extended guarding periods, so they must leave eggs to forage; 2) males actively guard the eggs at a distance during the day and protect them from conspecifics or other predators; and 3) males use the time away from guarding the eggs to search for additional mates. Additional field studies that involve monitoring the behavior of males guarding egg batches as well as the survival of egg batches that are guarded and unguarded (through male removal) are needed to assess the efficacy of paternal care in this species.

In most species of harvestmen, eggs grow larger and change color during development, gradually darkening before hatching (Gnaspini 2007). In gonyleptid harvestmen that oviposit on the undersurface of leaves, the first eggs that are laid by females are closest to the apex (Machado et al. 2004). On the basis of the position of the eggs and their different sizes and colors, we infer that these males guard batches of eggs through several developmental stages. We also infer that eggs at different stages of development are the result of different oviposition events, by one or more females. In 11 species of gonyleptoid harvestmen, males mate multiple times and guard eggs produced by multiple females (Machado & Macías-Ordóñez 2007). Thus, we hypothesize that the cosmetid species in our study also exhibits a polygynic mating system. Additional field studies that

involve the mark-recapture of females in the vicinity of guarding males are needed to assess this hypothesis.

We thank A. Solís for assistance with collecting and observing harvestmen in the field. We are especially thankful to Daniel Santamaria for help with the plant identifications. We also thank R. Macías-Ordóñez and an anonymous reviewer for insightful comments on an earlier version of the manuscript. This research was supported by a VWC Summer Faculty Development Grant (VRT), a Batten Endowed Professorship (VRT), and the VWC Science Undergraduate Research Fund. Specimens from Volcán Cacao were collected under MINAET permit no. 01228 (CV) and were exported to the U.S. under scientific passport no. 01607 (VRT). Voucher specimens of adult specimens will be deposited in the collections of INBio and American Museum of Natural History.

LITERATURE CITED

Canals, J. 1936. Observaciones biológicas en arácnidos del orden Opiliones. Revista Chilena Historia Natural 40:61–63.

Cokendolpher, J.C. & S.R. Jones. 1991. Karyotype and notes on the male reproductive system and natural history of the harvestman *Vonones sayi* (Simon) (Opiliones, Cosmetidae). Proceedings of the Entomological Society of Washington 93:86–91.

Forster, R.R. 1954. The New Zealand harvestmen (sub-order Laniatores). Canterbury Museum Bulletin 2:1–329.

Friebe, B. & J. Adis. 1983. Entwicklungzyklen von Opiliones (Arachnida) im Schwazwasser-Überschwemmungswald (Igapó) des Rio Tarumã Mirim (Zentralamazonien. Brasilien). Amazoniana 8:101–110.

Goodnight, C.J. 1958. Two representatives of a tropical suborder of opilionids (Arachnida) found in Indiana. Proceedings of the Indiana Academy of Sciences 67:322–323.

Goodnight, M.L. & C.J. Goodnight. 1976. Observations on the systematics, development, and habits of *Erginulus clavotibialis* (Opiliones: Cosmetidae). Transactions of the American Microscopical Society 95:654–664.

Gnaspini, P. 2007. Development. Pp. 455–472. *In* Harvestmen: The Biology of Opiliones. (R. Pinto-da-Rocha, G. Machado & G. Giribet, eds.). Harvard University Press, Cambridge, Massachusetts.

Hara, M.R., P. Gnaspini & G. Machado. 2003. Male guarding behavior in the Neotropical harvestman *Ampheres leucopheus* (Mello-Leitão, 1922) (Opiliones, Laniatores, Gonyleptidae). Journal of Arachnology 31:441–444.

Hunter, R.K., D.N. Proud, J.A. Tibbetts, J.A. Burns & V.R. Townsend, Jr. Parental care in the neotropical harvestman *Phareicranaus calcariferus* (Opiliones, Laniatores, Cranaidae). Journal of Arachnology 35:199–201.

Juberthie, C. 1972. Reproduction et développement d'un opilion Cosmetidae, *Cynorta cubana* (Banks) de Cuba. Annales Spéléologie 27:773–785.

Kury, A.B. & R. Pinto-da-Rocha. 1997. Notes on the Brazilian harvestmen genera Progonyleptoidellus Piza and Iporangaia Mello-Leitão. Revista Brasileira de Entomologia 41:109–115.

Machado, G. 2007. Maternal or paternal egg guarding? Revisiting parental care in triaenonychid harvestmen (Opiliones). Journal of Arachnology 35:202–204.

Machado, G. & R. Macías-Ordóñez. 2007. Reproduction. Pp. 414–454. *In* Harvestmen: The Biology of Opiliones. (R. Pinto-da-Rocha, G. Machado & G. Giribet, eds.). Harvard University Press, Cambridge, Massachusetts.

Machado, G. & P.S. Oliveira. 1998. Reproductive biology of the Neotropical harvestman *Goniosoma longipes* (Arachnida, Opiliones, Gonyleptidae): mating and oviposition behaviour, brood mortality, and parental care. Journal of Zoology 246:359–367.

Machado, G. & P.S. Oliveira. 2002. Maternal care in the Neotropical harvestman *Bourguyia albiornata* (Arachnida, Opiliones): oviposition site selection and egg protection. Behaviour 139:1509–1524.

Machado, G. & R.L.G. Raimundo. 2001. Parental investment and the evolution of subsocial behaviour in harvestmen (Arachnida Opiliones). Ethology Ecology & Evolution 13:133–150.

Machado, G., G.S. Requena, B.A. Buzatto, F. Osses & L.M. Rossetto. 2004. Five new cases of paternal care in harvestmen (Arachnida: Opiliones): implications for the evolution of male guarding in the Neotropical family Gonyleptidae. Sociobiology 44:577–598.

Machado, G. & J. Warfel. 2006. First case of maternal care in the family Cranaidae (Opiliones, Laniatores). Journal of Arachnology 34:269–272.

Martens, J. 1993. Further cases of paternal care in Opiliones (Arachnida). Tropical Zoology 6:97–107.

Mitchell, R.W. 1971. Egg and young guarding by a cave-dwelling harvestman, *Hoplobunus boneti* (Arachnida). Southwestern Naturalist 15:392–395.

Mora, G. 1990. Paternal care in a Neotropical harvestman, *Zygopachylus albomarginis* (Arachnida, Opiliones: Gonyleptidae). Animal Behavior 39:582–593.

Nazareth, T.M. & G. Machado. 2009. Reproductive behavior of *Chavesincola inexpectabilis* (Opiliones, Gonyleptidae) with description and independently evolved case of paternal care in harvestmen. Journal of Arachnology 37:127–134.

Nazareth, T.M. & G. Machado. 2010. Mating system and exclusive postzygotic paternal care in a Neotropical harvestman (Arachnida: Opiliones). Animal Behaviour 79:547–554.

Pinto-da-Rocha, R. 2002. Systematic review and cladistic analysis of the Caelopyginae (Opiliones, Gonyleptidae). Arquivos de Zoologia 36:357–464.

Rodriguez, C.A. & S. Guerrero. 1976. La historia natural y el comportamiento de *Zygopachylus albomarginis* (Chamberlin) (Arachnida: Opiliones: Gonyleptidae). Biotropica 8:242–247.

Townsend, V.R. Jr., C. Víquez, P.A. VanZandt & D.N. Proud. 2010. Key to the Cosmetidae (Arachnida, Opiliones) of Central America, with notes on penis morphology and sexual dimorphisms. Zootaxa 2414:1–26.

Manuscript received 21 May 2011, revised 10 August 2011.

2011. The Journal of Arachnology 39:500–502

SHORT COMMUNICATION

First record of paternal care in the family Stygnidae (Opiliones: Laniatores)

Osvaldo Villarreal Manzanilla: Museo del Instituto de Zoología Agrícola, Facultad de Agronomía, Universidad Central de Venezuela, Apartado 2101-A, ZP 4579, Maracay, Estado Aragua, Venezuela

Glauco Machado[1]: Departamento de Ecologia, Instituto de Biociências, Rua do Matão, Travessa 14, n° 321, Cidade Universitária, 05508-900, São Paulo, SP, Brazil

Abstract. Two cases of paternal care are described for species of the genus *Stenostygnellus* (Stygnidae), *S. flavolimbatus* Roewer 1913 and *S.* aff. *flavolimbatus*, both from Venezuela. Males of both species guard multiple clutches containing a large number of eggs, which are laid under rotting logs (*S. flavolimbatus*) or in the base of palm petioles (*S.* aff. *flavolimbatus*). These records probably represent a new and independently evolved case of paternal care in harvestmen.

Keywords: Egg-hiding, *Eutimesius*, maternal care, *Protimesius*, *Stenostygnellus*

Exclusive post-zygotic paternal care is regarded as the rarest form of parental investment among arthropods, being reported for only 17 lineages (Tallamy 2000, 2001; Nazareth & Machado 2010). Over half of the reports of independent evolution of paternal care in arthropods occurred in the order Opiliones, a group of arachnids with nearly 6500 described species (Kury 2003). Contrary to maternal care, which is restricted in harvestmen to species of the Neotropical superfamily Gonyleptoidea (Machado 2007; Machado & Macías-Ordóñez 2007), paternal care has evolved in at least four superfamilies of the suborder Laniatores: once in the Triaenonychoidea (family Triaenonychidae), once in the Samoidea (family Podoctidae), once in Assamioidea (family Assamiidae), and at least three times in the Gonyleptoidea (family Gonyleptidae) (references in Machado et al. 2004; Machado 2007; Nazareth & Machado 2009). In this paper, we report for the first time paternal care in representatives of Stygnidae and also offer anecdotal behavioral information on other species in order to discuss the evolution of the different forms of parental care in this family.

We made opportunistic observations of paternal behavior during two field expeditions devoted to the collection of arachnological material in Venezuela. The two species we studied belong to the genus *Stenostygnellus* Roewer (Heterostygninae), a small group of Neotropical harvestmen restricted to forested areas in the northern mountains of Venezuela. Although only two species are currently recognized in the genus, *S. flavolimbatus* Roewer 1913 and *S. macrochelis* (Roewer 1917) (see Pinto-da-Rocha 1997), the systematics of the group deserve further study (Villarreal 2007). We found the first species, *S. flavolimbatus*, at the El Ávila National Park (10°31′5.95″N, 66°48′21.87″W; ca 1700 m elev.), Distrito Capital, Venezuela. We observed this species along the trail between the Humboldt Hotel and the La Silla del Ávila in July 2006. The second species, identified as *S.* aff. *flavolimbatus*, is probably a new species (O. Villarreal-Manzanilla unpublished data). We observed this species in a cloud forest near Colonia Tovar (10°24′56.30″N, 67°17′12.64″W; ca 2000 m elev.), state of Aragua, in July 2008. Voucher specimens of males are deposited in the arachnological collection of the Museo del Instituto de Zoología Agrícola (MIZA), Maracay, Venezuela.

We found two males of *S. flavolimbatus* guarding clutches of eggs nearly 50 cm from each other in a cavity in a large rotting log. Both males were resting close to a clutch containing more than 100 eggs in different stages of embryonic development (based on differences of color and size). We interpret the presence of the males close to the clutches as parental care because both males maintained the typical posture exhibited by parental individuals in other harvestman species (see Machado et al. 2004; Machado & Warfel 2006). The presence of eggs in different stages of embryonic development, which is common among harvestmen exhibiting exclusive paternal care (Machado et al. 2004; Machado & Macías-Ordóñez 2007), suggests that guarding males accept eggs from more than one female or from the same female at different times.

We also found one male and one female of *S.* aff. *flavolimbatus* close to a clutch laid in the base of a palm petiole. The clutch contained nearly 150 eggs in at least two different stages of embryonic development, and the eggs were in multiple layers (Fig. 1A) – a pattern of egg deposition only described for another species with paternal care, the assamiid *Lepchana spinipalpis* (Martens 1993). When we photographed the clutch, both individuals were disturbed, but only the female abandoned the oviposition site. The male remained close to the clutch and constantly tapped the eggs with his second pair of legs (Fig. 1A). We interpret the presence of the male close to the eggs as parental care because the individual did not abandon the clutch after disturbance. Moreover, the male inspected the clutch after disturbance with his sensorial legs, like parental individuals of other harvestman species usually do after disturbance (e.g., Mora 1990; Machado et al. 2004). The presence of a female close to the clutch, on the other hand, does not necessarily indicate biparental care because harvestman females usually remain for some time at the oviposition site, both before and after egg laying (Mora 1990; Nazareth & Machado 2009, 2010).

The only previously studied species of Stygnidae is the Amazonian *Auranus parvus* Mello-Leitão 1941 (Stygninae), which lays its eggs inside fissures on the bark and provides no further care (Friebe & Adis 1983). Laboratory observations on two other Amazonian Stygninae, *Stygnus* sp. and *Protimesius longipalpis* (Roewer 1943), indicate that females also hide their eggs inside fissures in rotting logs and do not provide additional care to the offspring (G. Machado unpublished data). Given the phylogenetic position of the genera *Auranus*, *Stygnus*, and *Protimesius* within the Stygninae (Pinto-da-Rocha 1997; Pinto-da-Rocha & Villarreal-Manzanilla 2009), the plesiomorphic form of parental care in the subfamily is probably egg-hiding.

Our observations on *Stenostygnellus* spp. are the only reproductive data for the subfamily Heterostygninae. In March 2004, however, we received a photo of a stygnid harvestman from Tiputini

[1] Corresponding author: E-mail: glaucom@ib.usp.br

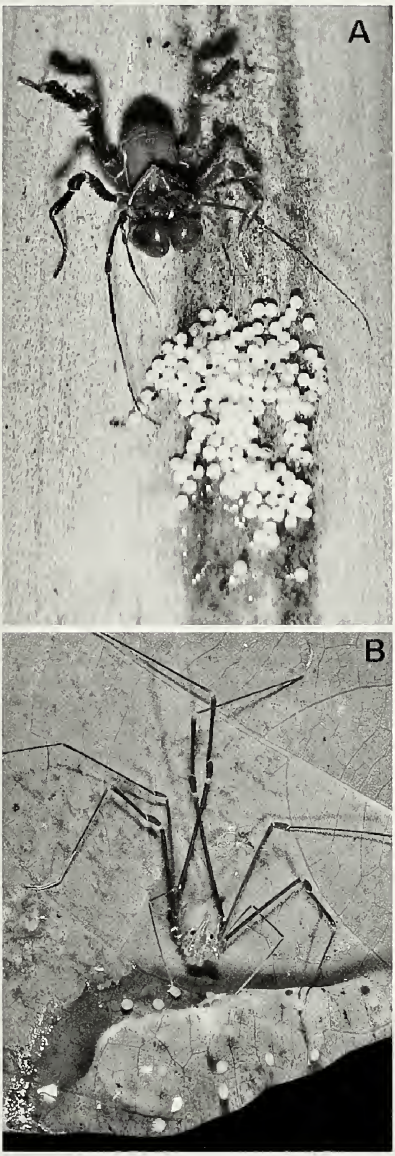


Figure 1.—A. Male of *Stenostygnellus* aff. *flavolimbatus* close to a multiple clutch laid on the petiole of a palm. The guarding male is touching the eggs with his second pair of legs (photo: O. Villarreal). B. Female of *Eutimesius* sp. prostrated close to eggs laid on a leaf and surrounded by an abundant mucus coat (photo: Bejat McCracken).

Biodiversity Station, Ecuador, probably caring for eggs imbedded in an abundant mucus coat (Fig. 1B). We unequivocally identified the individual, which almost certainly belongs to the genus *Eutimesius* Roewer 1913, as being a female, based on the relative small size of the chelicerae and the lack of apical spines on femur IV (see Pinto-da-Rocha 1997). Anecdotal field observations indicate that the female remained close to the clutch for some days and did not consume the eggs (B. McCracken pers. comm.), which we interpret as probable maternal care. The genus *Eutimesius* is the sister group of the clade formed by the genera *Stygnoplus* + *Stenostygnellus* (Pinto-da-Rocha 1997). Unfortunately, the lack of behavioral data on the basal lineages of Heterostygninae, as well as on the monotypic Nomoclastinae, makes it difficult to present a hypothesis for the evolution of the different forms of parental care in Stygnidae. Nevertheless, it is likely that the cases of post-zygotic parental care we describe represent independent events of evolution of both maternal and paternal assistance in harvestmen of the superfamily Gonyleptoidea.

ACKNOWLEDGMENTS

We thank Bejat McCracken for allowing us to use the photo included here as Fig. 1B and for some behavioral information on the species. We also thank Billy Requena, Bruno Buzatto, Linden Higgins, and two anonymous reviewers for helpful comments on the manuscript. GM is supported by fellowships from Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP, 02/00381-0; 08/54833-5) and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior.

LITERATURE CITED

Friebe, B. & J. Adis. 1983. Entwicklungzyklen von Opiliones (Arachnida) im Schwarzwasser-Überschwemmungswald (Igapó) des Rio Tarumã Mirim (Zentralamazonien, Brasilien). Amazoniana 8:101–110.

Kury, A.B. 2003. Annotated catalogue of the Laniatores of the New World (Arachnida, Opiliones). Revista Ibérica de Aracnología, volume especial monográfico 1:1–337.

Machado, G. 2007. Maternal or paternal egg guarding? Revisiting parental care in triaenonychid harvestmen (Opiliones). Journal of Arachnology 35:202–204.

Machado, G. & R. Macías-Ordóñez. 2007. Reproduction. Pp. 414–454. *In* Harvestmen: the Biology of Opiliones. (R. Pinto da Rocha, G. Machado & G. Giribet, eds.). Harvard University Press, Cambridge, Massachusetts.

Machado, G., G.S. Requena, B.A. Buzatto, F. Osses & L.M. Rossetto. 2004. Five new cases of paternal care in harvestmen (Arachnida: Opiliones): implications for the evolution of male guarding in the Neotropical family Gonyleptidae. Sociobiology 44:577–598.

Machado, G. & J. Warfel. 2006. First case of maternal care in the family Cranaidae (Opiliones: Laniatores). Journal of Arachnology 34:269–272.

Martens, J. 1993. Further cases of paternal care in Opiliones (Arachnida). Tropical Zoology 6:97–107.

Mora, G. 1990. Parental care in a neotropical harvestman, *Zygopachylus albomarginis* (Arachnida: Gonyleptidae). Animal Behaviour 39:582–593.

Nazareth, T.M. & G. Machado. 2009. Reproductive behavior of *Chavesincola inexpectabilis* (Opiliones: Gonyleptidae), with the description of a new and independently evolved case of paternal care in harvestman. Journal of Arachnology 37: 127–134.

Nazareth, T.M. & G. Machado. 2010. Mating system and exclusive post-zygotic paternal care in a neotropical harvestman (Arachnida: Opiliones). Animal Behaviour 79:547–554.

Pinto-da-Rocha, R. 1997. Systematic review of the neotropical family Stygnidae (Opiliones, Laniatores, Gonyleptoidea). Arquivos de Zoologia 33:163–342.

Pinto-da-Rocha, R. & O. Villarreal-Manzanilla. 2009. Cladistic analysis of the Stygninae and description of a new species of *Protimesius* Roewer, 1913 (Opiliones: Stygnidae). Zootaxa 2176:48–56.

Tallamy, D.W. 2000. Sexual selection and evolution of exclusive paternal care in arthropods. Animal Behaviour 60:559–567.

Tallamy, D.W. 2001. Evolution of exclusive paternal care in arthropods. Annual Review of Entomology 46:139–165.

Villarreal, M.O. 2007. Notes on the genus *Stenostygnellus* Roewer (Opiliones: Stygnidae) in Venezuela. Pp. 123. *In* Abstract, 17 International Congress of Arachnology. (A.D. Brescovit & G. Machado, eds.). FAPESP, São Pedro, São Paulo, Brazil.

Manuscript received 24 March 2011, revised 13 June 2011.

2011. The Journal of Arachnology 39:503–505

SHORT COMMUNICATION

Aggregations of *Sphodros rufipes* (Araneae: Atypidae) in an urban forest

Steven B. Reichling[1], **Christopher Baker**[1] and **Christina Swatzell**[2]: [1]Memphis Zoo, 2000 Prentiss Place, Memphis, Tennessee 38112 USA; [2]Pace Law School, 78 North Broadway, White Plains, New York 10603 USA. E-mail: sreichling@memphiszoo.org

Abstract. A large population of *Sphodros rufipes* (Latreille 1829) was discovered in a municipal park in Memphis, Tennessee. We examined potential stem diameter preference, frequency of web attachment to available tree species and the spatial distribution patterns of spiders and potential attachment structures. A wide range of structure diameters were utilized for web attachment. The association of pursewebs to tree taxa was independent of the frequency of tree taxa occurrence. The spacing of vegetation stems and trunks was approximately random, but spiders exhibited a nonrandom, aggregated distribution, which was more pronounced in subadults than adults. The factors influencing *S. rufipes* to occur in aggregations cannot be explained by the spatial proximity of potential attachment structures in the forest.

Keywords: Purseweb spider, random distribution, aggregations, density, tree preference

Sphodros is one of three genera that comprise the mygalomorph family Atypidae. Five species are confined to the United States (Gertsch & Platnick 1980), with *Sphodros rufipes* (Latreille 1829) being the most widespread and known from scattered locations throughout the eastern United States (Hoffman 1992). The species has been described as uncommon throughout most of its range (Hardy 2003), but occasionally may be locally abundant (Poteat 1889; Morrow 1986; Mckenna-Foster et al. 2011). As the widest-ranging *Sphodros* spider, *S. rufipes* is also the best studied. The seasonality of reproductive behaviors is well documented (McCook 1888; Coyle & Shear 1981; Morrow 1986), as is the timing and pattern of post-embryonic development (Coyle & Shear 1981). The architecture of the purseweb has been thoroughly described (Bishop 1950; Gertsch & Platnick 1980; Coyle & Shear 1981; Beatty 1986; Morrow 1986; Hardy 2003). However, its population biology is poorly documented, probably due to its generally sparse occurrence and cryptic webs. Previous studies have reported population densities (Poteat 1889; Coyle & Shear 1981), but only one has described spatial patterns (Mckenna-Foster et al. 2011).

Although authors frequently note the tree species to which *Sphodros* webs are attached, only Hardy (2003) has analyzed tree species association, reporting a higher frequency (58%) of attachment to oaks (*Quercus* spp.) and sweet gum (*Liquidambar*) and the avoidance of conifers and herbaceous vegetation. Muma (1944) stated that *S. rufipes* preferred small trees for web attachment, an observation that was supported by Coyle and Shear's (1981) data indicating a mean trunk diameter of 10.4 cm. Hardy (2003) pursued this topic and found no webs attached to trunks larger than 65 cm diameter-at-breast-height (dbh). The populations studied by Mckenna-Foster et al. (2011) were unusual due to the majority of the webs being attached to grasses and other non-woody structures.

From these studies, a picture develops of a spider that typically attaches its web to the trunks of sapling or small hardwoods, within an environment that offers a wider variety of potentially suitable structures. Interesting questions then emerge. How constrained are the spiders to utilize web supports in close proximity to conspecifics, given their proclivity for specific types of attachment points which may themselves be spaced according to other environmental factors? Is the spacing of *Sphodros* webs solely a reflection of the arrangement of suitable supports? No previous study has examined these potential dynamics.

Following the fortuitous discovery of a male *S. rufipes* wandering the forest floor of a city park, subsequent surveys revealed a surprising abundance of purseweb spiders, encouraging further study. This large population presented a unique opportunity to examine, for the first time, spatial distribution patterns of a purseweb spider population. The purpose of our study was to measure the density of *S. rufipes* in an urban forest island, characterize spatial patterns, and to consider these patterns in light of the spacing, size, and taxa of indigenous web-supporting vegetation.

The research was conducted during June–August 2009, in a 28.7 ha mature hardwood forest within Overton Park, Memphis, Tennessee, which became an isolated fragment when the urban expansion of Memphis encircled it by 1906 (Gilbert 1992). We inventoried and identified every tree $\geq$ 7.62 cm dbh within an 800 m^2 portion of the park after broad surveys indicated it was representative of the whole. Subsequent analysis of web attachment frequency to tree taxa was performed at the generic level because the structural characteristics encountered by the spiders, such as bark texture, and thus the biological relevance, would be distinct.

To determine the range of structure size chosen by the spiders, we measured stem diameter at 25 cm above the ground surface, from a random forest-wide sample of 186 plants and trees with one or more attached pursewebs. We chose this measurement instead of the dbh-standard of forestry science because the latter was less relevant to *Sphodros* behavior than diameter at the level where the spiders would encounter the structures and attach their webs.

To describe spatial patterns of *Sphodros*, three 12 × 12 m quadrats were established. Since we were interested in discovering how *Sphodros* position themselves in relation to nearby conspecifics and suitable web-supporting vegetation, selection of transect positions was not random. Instead, we established each transect at a location where broad surveys of the entire park identified high spider density. At each transect, we meticulously inspected the ground for all *Sphodros* webs, including the smallest juveniles, of which there were many, and we are confident that all webs were found. Each web was categorized as being occupied by an adult versus a subadult on the basis of diameter. Webs $\geq$ 12 mm were classified as adult. This criterion resulted in two discrete groups, with an obvious size gap between the adult threshold size and the largest subadult webs.

We quantified spatial distribution of *Sphodros* pursewebs using the methods of Morisita (1959). For each transect, we reiterated the calculation of Morista's Index (I_δ) for 1, 2, 4 and 6 m^2 quadrants, and observed for changes in the distribution pattern. Measuring spatial pattern at multiple scales is essential because aggregations are a function of the scale at which they are viewed. For each quadrant size,

Table 1.—List of trees (n = 1985) by genus with their relative frequency and mean dbh (cm) and the number of associated *Sphodros rufipes* webs.

Genus	DBH (SE)	Percent occurrence	Webs
Acer	17.8 (0.7)	10.28	9
Aesculus	7.6 (0.4)	0.65	0
Albizia	14.5 (1.7)	0.55	0
Asimina	10.2 (2.9)	35.11	9
Betula	16.1 (2.11)	0.16	0
Carpinus	14.4 (0.8)	1.91	5
Carya	18.9 (1.0)	8.87	5
Cercis	19.1 (3.2)	1.36	0
Celtis	21.3 (2.8)	1.01	0
Cornus	18.8 (2.3)	1.21	1
Fraxinus	34.5 (3.1)	2.42	1
Juniperus	6.0 (1.8)	0.20	1
Liquidambar	36.3 (2.0)	5.44	3
Liriodendron	65.7 (4.7)	3.73	4
Morus	14.0 (2.8)	0.20	0
Quercus	69.2 (2.7)	8.16	22
Sassafras	20.3 (1.6)	1.26	0
Ulmus	16.3 (0.4)	17.48	22
Total		100.00	82

index values < 1 occur when distribution is hyperdispersed and > 1 when underdispersed (Vandermeer 1990). An abrupt change in the index value between two quadrant sizes denotes the approximate area encompassed by the aggregations (Vandermeer 1990).

We identified 1,985 trees, composed of 30 species of 21 genera (*Acer negundo*, *A. rubrum*, *A. saccharum*, *Aesculus sylvatica*, *Albizia julibrissin*, *Asimina triloba*, *Betula papyrifera*, *Carpinus caroliniana*, *Carya glabra*, *C. illinoensis*, *C. tomentosa*, *Cercis canadensis*, *Celtis occidentalis*, *Cornus florida*, *Fraxinus americana*, *Liquidambar styracifolia*, *Liriodendron tulipifera*, *Morus rubra*, *Nyssa sylvatica*, *Platanus occidentalis*, *Populus deltoides*, *Prunus serotina*, *Quercus alba*, *Q. falcata*, *Q. rubra*, *Q. schumardii*, *Q. velutina*, *Sassafras albidum*, *Ulmus americana*, and *U. rubra*).

The majority (65%) of tree genera occurring in Overton Park were utilized by *S. rufipes* as purseweb supports (Table 1). A large proportion (20%) of spiders utilized small herbaceous plants as web supports, as depicted in Fig. 1. We also observed *Sphodros* utilizing miscellaneous ground litter as supports, such as fallen dead leaves and limbs (9%). A few webs (6%) were not supported by any structure; i.e., were aligned horizontally upon the forest floor, as is more characteristic of the Old World *Atypus* (Gertsch & Platnick 1980), or were partially attached to fallen debris.

The diameter of 186 vegetation stems or trunks supporting pursewebs ranged widely (0.01–268.0 cm, mean = 47.2 cm, SE = 20.5). The diameters of stems with webs containing subadults (n = 170) did not differ significantly (X^2_1 = 0.13, P = 0.73, from those supporting webs of adults (n = 16).

The frequency of *Sphodros* webs among tree genera was significantly different (X^2_{17} = 70.4, $P < 0.0001$) than the distribution of tree genera within the total population in the study site. *Ulmus* and *Quercus* were the sites of attachment for the majority (54%) of adult-occupied webs. Seven tree genera were not observed to have webs attached. Among trees supporting at least one purseweb, *Cornus*, *Fraxinus*, and *Juniperus* were the least frequently utilized by spiders.

A total of 853 pursewebs were counted in the three transects. Webs occupied by adults comprised 4% of the sample (n = 36, transect range 10–14) versus subadults (n = 817, transect range 152–504). The mean density of adults was 0.08/m^2 and mean density of subadults was 1.9/m^2.

Figure 1.—*Sphodros rufipes* web utilizing a small herbaceous sprout as support.

The spatial distribution of stems and tree trunks was approximately random in both the broad landscape and smaller transect perspective. Within the 12 m^2 transects, I_δ ranged from 1.0–1.6 (mean = 1.2). Spatial arrangement of adult and subadult classes in the 12 m^2 transects indicated aggregation (Fig. 2). For adults in each transect, I_δ min/max values were 1.2–2.2, 1.3–2.1, and 0.9–1.6 (calculated for 2, 4, and 6 m^2 quadrants only due to small sample size). For subadults, min/max of I_δ were 1.0–2.0, 2.6–6.5, and 1.1–2.6.

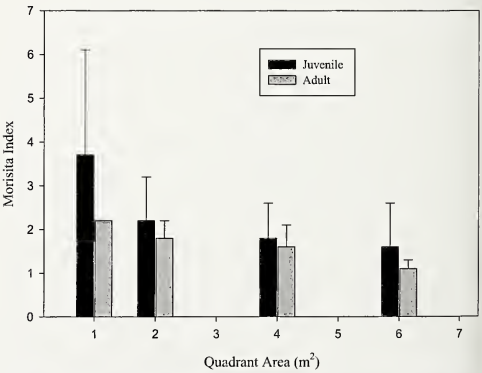


Figure 2.—Mean (+ SE) values of Morisita Index for subadult and adult subclasses of *Sphodros rufipes* at 1, 2, 4, and 6 m^2 quadrat size in three 144 m^2 quadrats. Adults in the 1 m^2 quadrant consisted of a single individual.

Though purseweb spiders aggregate, the available support structures are both abundant and randomly positioned. Thus, the spiders are not underdispersed as an artifact of the spatial constraints of suitable attachment sites. It is tempting to hypothesize that juvenile purseweb spiders are displaying colonial attraction to each other by their close proximity. An alternative explanation, which we favor, is that the poor dispersal capabilities of the spiderlings restrict them to settle into high-density groups, composed primarily or completely of siblings. We propose that these high densities, and the competition for prey and other limited resources that they engender, represent suboptimal conditions for the spiders, which is gradually alleviated by fitness-based mortality.

We measured a density that was ten times greater than the previously highest measure documented for the genus (Mckenna-Foster et al. 2011). In most states where it occurs, *Sphodros* is listed either as rare or as a species of concern (Anonymous 2004; Roble 2006). Commenting on the status of *S. coylei* Gertsch & Platnick 1980, Wolff (2005) speculated that *Sphodros* may require large areas of habitat to survive, that urbanization was the primary threat to the genus in most areas, and that isolated populations might not have long-term viability. Therefore it is noteworthy that in a small fragment of forested habitat, isolated for over a century and embedded within an urban landscape, *S. rufipes* is abundant.

We thank Andy Kouba, Jon Davis, Fields Falcone, Stephanie Cassel, Lauren Lieb, Cybil Covic, and Mitch Taylor for sharing tree data. Chellie Bowman assisted us in the forest surveys. Alan Jaslow and Erin Willis lent statistical guidance. The Memphis Zoological Society provided time and equipment to conduct this study.

LITERATURE CITED

Anonymous. 2004. Current and historical rare, threatened, and endangered species of Calvert County, Maryland. Maryland Dept. of Natural Resources, Wildlife and Heritage Service, Annapolis, Maryland.

Beatty, J.A. 1986. Web structure and burrow location of *Sphodros niger* (Hentz) (Araneae, Atypidae). Journal of Arachnology 14: 130–132.

Bishop, S.C. 1950. The purse-web spider *Atypus abbotti* (Walckenaer) with notes on related species (Arachnidae: Atypidae). Entomological News 61:121–124.

Coyle, F.A. & W.A. Shear. 1981. Observations on the natural history of *Sphodros abbotti* and *Sphodros rufipes* (Araneae, Atypidae) with evidence for a contact sex pheromone. Journal of Arachnology 9:317–326.

Gertsch, W.J. & N.I. Platnick. 1980. A revision of the American spiders of the family Atypidae (Araneae, Mygalomorphae). American Museum Novitates 2704:1–39.

Gilbert, D. 1992. The old forest. Memphis Magazine 17(7):36–41, 66–71.

Hardy, L.M. 2003. Trees used for tube support by *Sphodros rufipes* (Latreille 1829) (Araneae, Atypidae) in northwestern Louisiana. Journal of Arachnology 31:437–440.

Hoffman, R.L. 1992. Purse-web spiders (Atypidae) in Virginia (Araneidae: Mygalomorphae). Banisteria 1:5–7.

McCook, H.C. 1888. Nesting habits of the American purseweb spider. Proceedings of the Philadelphia Academy of Natural Science 40:203–220.

Mckenna-Foster, A., M.L. Draney & C. Beaton. 2011. An unusually dense population of *Sphodros rufipes* (Mygalomorphae: Atypidae) at the edge of its range on Tuckernuck Island, Massachusetts. Journal of Arachnology 39:171–173.

Morisita, M. 1959. Measuring the dispersion of individuals and analysis of the distributional patterns. Memoirs of the Faculty of Science, Kyushu University Series Biology 2:215–235.

Morrow, W. 1986. A range extension of the purseweb spider. Journal of Arachnology 14:119.

Muma, M.H. 1944. A report on Maryland spiders. American Museum Novitates 1257:1–14.

Poteat, W.L. 1889. A tube-building spider. Journal of the Elisha Mitchell Scientific Society 6:134–147.

Roble, S.M. 2006. Natural heritage resources of Virginia: rare animals. Virginia Department of Conservation and Recreation, Division of Natural Heritage, Richmond, Virginia.

Vandermeer, J. 1990. Elementary Mathematical Ecology. Krieger Publishing Co., Malabar, Florida.

Wolff, R.J. 2005. Coyle's purseweb spider *Sphodros coylei*. Comprehensive Wildlife Conservation Strategy, South Carolina Department of Natural Resources, Columbia, South Carolina.

Manuscript received 5 May 2010, revised 30 August 2011.

2011. The Journal of Arachnology 39:506–510

SHORT COMMUNICATION

Bringing spiders to the multilocus era: novel anonymous nuclear markers for *Harpactocrates* ground-dwelling spiders (Araneae: Dysderidae) with application to related genera

Leticia Bidegaray-Batista[1], **Rosemary G. Gillespie**[2] and **Miquel A. Arnedo**[1]: [1]Institut de Recerca de la Biodiversitat & Departament de Biologia Animal, Universitat de Barcelona, Avenida Diagonal 643, 08020, Barcelona, Spain. E-mail: letigaray@yahoo.com; [2]Department of Environmental Science Policy and Management, University of California, 137 Mulford Hall, Berkeley, California 94720-3114

Abstract. Multilocus approaches are essential for accurately recovering the evolutionary processes underlying species and population history. However, historical inferences in non-model organisms are still almost exclusively based on mitochondrial DNA due to the difficulty of obtaining multiple informative loci. Here, we use a genomic library based approach, to generate 15 novel anonymous nuclear markers (ANMs) from the ground spider *Harpactocrates globifer* Ferrández 1986. The ANMs cross-amplify and sequence well in the target species and its two closest relatives, and some of them also in the more distantly related *H. ravastellus* Simon 1914. Levels of nucleotide diversity of the ANMs within *H. globifer* ranged from 0.05% to 1.4% and average sequence divergence between close congeneric relatives from 0.02% to 13.9%, supporting the utility of these loci in population and species-level analyses. Moreover, a cross-species amplification screened in other spider taxa showed that some of the loci could also potentially be useful in more distantly related genera.

Keywords: Genomic library, nuclear loci, multilocus approaches, non-model organisms

Multilocus approaches based on unlinked markers, including both mitochondrial (mtDNA) and nuclear markers, are essential for an accurate reconstruction of the evolutionary processes underlying species and population history. Inferences based exclusively on mtDNA markers are hampered by processes such as sex-biased behaviors (e.g., sex-biased dispersal), low dispersal ability and small population sizes, incomplete lineage sorting, introgression or selective sweeps (Avise 2000; Hare 2001; Irwin 2002; Ballard & Whitlock 2004; Wilkins 2004; Kuo & Avise 2005). In recent years the realization that gene trees and species trees can differ markedly in closely related species has sparked the development of a new generation of methods for species tree inference, which rely strongly on the information provided by multiple markers (Maddison 1997; Edwards 2009). Moreover, many studies have shown that the statistical power of parameters such as divergence times, population size and rates of gene flow, rely on the number of loci used (see Brumfield et al. 2003; Brito & Edwards 2009 and references therein). Recent advances, both technological (see reviews of Hudson 2007; Thomson et al. 2010; Ekblom & Galindo 2011) and methodological (e.g., Hey & Nielsen 2007; Heled & Drummond 2010; Hey 2010; Yang & Rannala 2010), have greatly facilitated the implementation of multilocus analyses. Unfortunately, the scarcity of available genomic information makes finding multiple informative loci in non-model organisms a daunting task (Thomson et al. 2010). This is especially true for spiders, in which just a handful of mitochondrial and nuclear markers that are variable at the population and species level can be reliably amplified and sequenced (see e.g., Hedin 1997 for nad1; Maddison & Hedin 2003 for nad1, 16S and EF-1 alpha; Ayoub et al. 2007 for EF-1 gamma; Bidegaray-Batista et al. 2007 for cox1 and 16S-nad1 fragment; Bond & Stockman 2008 for 12S-16S fragment and ITS-1 and ITS-2; Vink et al. 2008 for Actin 5C; Garb & Gillespie 2009 for cox1, 16S-nad1 fragment and EF-1 alpha; Muster et al. 2009 for ITS-1, 5.8S rDNA and ITS-2; De Busschere et al. 2010 for cox1 and 28S).

Here, we report on a method to circumvent this limitation by isolating novel anonymous nuclear markers (ANMs) from a spider genomic library. Our target organisms are species belonging to the ground-dwelling genus *Harpactocrates* Simon 1914 (family Dysderidae) which inhabit the mountain ranges of the Sistema Central in the Iberian Peninsula. From west to east, the species *Harpactocrates gredensis* Ferrández 1986, *H. globifer* Ferrández 1986 and *H. gurdus* Simon 1914 are found along the range, showing narrow, almost non-overlapping distributions. As with other species (about 13) in the genus, they are generally found at high elevation (above 1000 m) in temperate and moist forests, suggesting a preference for cool and humid environments. Preliminary phylogenetic and phylogeographic studies have shown that Pleistocene glaciations had a major role in structuring populations in *Harpactocrates*. These observations have led us to hypothesize that *Harpactocrates* species in the Sistema Central underwent population range expansion toward lower elevations during cooler periods, facilitating gene flow, whereas at interglacial periods they retreated to high elevation refuges, which then led to population fragmentation (e.g., Masta 2000; Knowles 2001; DeChaine & Martin 2005; Carstens & Knowles 2007b; Mardulyn et al. 2009; Schmitt 2009). With the aim of testing this hypothesis using a multilocus species/population approach, we have developed 15 novel ANMs from a genomic library of *H. globifer*, which cross-amplify and sequence well in the closely related species *H. gurdus* and *H. gredensis* and some of them in a more distant species *H. ravastellus* Simon 1914. Additionally, we have screened cross-species amplification in other spider taxa in order to evaluate the range and potential application of the novel markers (see below).

We constructed a genomic library from the pooled DNA of two *H. globifer* specimens. Total genomic DNA was extracted using SpeedTools Tissue DNA extraction kit (Biotools) and concentrated via ethanol precipitations. Genomic DNA (~10 µg) was digested with EcoRI restriction enzyme (50 µL total volume). The enzyme was selected following the recommendations of Carstens & Knowles (2006). The goal was to ensure that the enzyme did not cut the mitochondrial DNA into fragments smaller than 1.6 kilobase pairs (kb), thereby reducing the likelihood of cloning mtDNA fragments. EcoRI was selected based on the information provided by a complete mitochondrial genome of a new species of *Parachtes* Alicata 1964 (pending formal description, Pons, Bidegaray-Batista & Arnedo unpublished data), which is the sister genus to *Harpactocrates*. Digested DNA was visualized on a 1% agarose gel stained with ethidium bromide, and fragments between 0.8 and 1.5 kb in length

Table 1.—Primer sequences for fifteen anonymous nuclear loci developed from a genomic library of *Harpatocrates globifer*. Names indicate the loci, forward and reverse primers, PCR annealing temperature T (°C), size of amplicon and GenBank Accession No. of the original cloned fragment. Performance codes indicate successful amplification in the following species: *H. globifer* (1), *H. gurdus* (2), *H. gredensis* (3) and *H. ravastellus* (4), *Parachtes romandiolae* (a), *Dysdera erythrina* (b), *Harpactea corticalis* (c), *Loxosceles rufescens* (d), *Troglohyphantes lucifuga* and *T. pedemontanus* (e), *Nemesia randa* and *Iberesia brauni* (f). PCR produets resulting in double bands (db) or multiple bands (mb) are indicated as superscripts.

Locus	Primer sequences (5′-3′)	T (° C)	Amplicon size (bp)	Accession no.	Performance
qgL1	F: AGACAGCATTCAGAGTCCAAGCG R2: GCCGAAATAGTTTGAGCTCGTTTGCG	56	416	JN654497	1,2,3,4, a^{mb}
qgL5	F: TGCCCACGCCCCACTAAAATAGG R: GCCAGGTTGCCAGTTAAAATCACG	58	424	JN654498	1,2,3,4, a, b
qgL10	F: AGCGACACATCCTTACCTGCGT R: GCGCATCTGGAGAGCCTTTGA	58	621	JN654506	1,2,3,4, a^{mb}, e
qgL12	F: TGGCACAGCAGTGGCCAGAA R: CATGTCAACCGAATAGAATC	55	617	JN654509	1,2,3
qgL21	F: ACGCCCGAACCGACCTTTGC R: ACGAGGGAGGTGCTAGAAGCG	58	580	JN654499	1,2,3, a^{db}, f^{mb}
qgL22	F: ACGATGCACCCTCGAAATGGTCG R: TTGGCGCGGAACCTCTCAGC	58	508	JN654511	1,2,3,4, a^{db}
qgL25	F: TGCCCACGCCACCCCTATCC R: AGGCCAACGCGAAAAGTCAGC	59	309	JN654510	1,2,3,4, a, b, d
qgL26	F: TCCCCGGGTCACGTGGGAAG R: TCCCCAACGTGAACGAACCGC	57	586	JN654500	1,2,3,4, a^{mb}
qgL28	F: GTCCCGTCGTCCGGGGTTTG R: GCCACCCATGCTTTTTGTGCTCC	59	401	JN654508	1,2,3,4, a
qgL29	F: TGGACTCCCGTTTCACAAGGCG R: CCACGCTATAATTGGCCCACAAGC	53	459	JN654502	1,2,3, a^{mb}
qgL32	F: AGCCCCAACATCCGTTTGACC R: CGTCGGCAAAAGGGACCACCC	58	567	JN654503	1,2,3,4, a^{mb}
qgL33	F: ACGTGCCACACTCTCTCTCTTTCG R: TGCCTGCTCGAATCAAACCCAGC	58	343	JN654504	1,2,3
qgL34	F: CGCGTCACCATAGGCTCTTCGC R: AGTTCGGTGTGTGGCCGAGC	58	408	JN654507	1,2,3, a^{mb}, b^{db}
qgL36	F: AGCGTAACGTAGGGCGTGCAG R: CGGCCGCTTGGAAGGTGGTC	58	627	JN654501	1,2,3,4, a^{mb}, b^{mb}, f^{db}
qgL38	F: TCACAGGCATACGAAAGCGCC R: GCCGAGCGTAGGCCTAGCATAAC	58	454	JN654505	1,2,3,4, a

were excised and purified from the gel using the kit QIAquick Gel Extraction kit (QIAGEN). Excised fragments were concentrated via ethanol precipitations to 8 ng/μL and cloned using the CloneJET™ PCR Cloning kit (Fermentas) and One Shot TOP10 competent cells (Invitrogen). Transformed cells were plated on agar plates containing ampicillin. Five hundred colonies were individually picked with a pipette tip and added directly to a 25 μL PCR mix containing the primers included in the cloning kit. Amplified inserts were visualized on a 1% agarose gel stained with ethidium bromide. Of the 500 amplified inserts, 206 that ranged in size from 300 to 1200 bp were selected for sequencing. Forty-one sequences were discarded because they were either identical to other sequences or did not sequence well. The remaining 165 sequences were locally blasted against the *Parachtes* sp. mitochondrial genome to ensure that there were no mtDNA sequences among the selected inserts, and in all cases they turned out to be part of the nuclear genome. Subsequently, we performed nucleotide BLAST searches against the GenBank database to characterize sequences. Most sequences (160 out of 165) reported non-significant BLAST hits. Thirty-eight of these sequences were subsequently selected for primer design based on features that ensured that they were non-coding regions, such as the presence of multiple stop codons in each of the six reading frames, and avoiding poly-A or -G runs, which are difficult to sequence. The primer pairs designed were initially screened in a set of individuals consisting of one from each of the three target species (*H. globifer*, *H. gurdus* and *H. gredensis*) and one belonging to a more distantly related species (*H. ravastellus* from the Pyrenees). Each primer pair was tested in a standard 25 μL PCR mix with the following conditions: 3 min at 94° C followed by 30 cycles of denaturation at 94° C for 30 s, annealing at three different temperatures of 52° C, 55° C and 58° C for 35 s, and extension at 72° C for 1 min, with a final single extension step of 72° C for 10 min. Of the 38 previously selected loci, 15 produced a single band product for at least one of the annealing temperatures tested and sequenced well in the three target species (Table 1). The annealing temperature of the PCR reaction was subsequently optimized (see Table 1), and the extension time was adjusted according to the length of the fragment.

Eight to 10 individuals of *H. globifer* from different populations were sequenced for each locus (Table 2) to investigate how informative the markers might be for population and phylogeographic studies. In addition, diversity indices and population statistics of the anonymous makers were compared with those of known mitochondrial genes and nuelear introns. With this aim, a mitochondrial fragment (*16S-nadl*) spanning the 3′ half of the 16S rRNA ribosomal subunit (*rrnL*), the complete tRNA leu (*trnL1*), the 5′ half of the NADH dehydrogenase subunit I (*nadl*) and the nuclear intron of the signal recognition particle 54-kDA subunit (*srp54*) were amplified and sequenced for 10 individuals of *H. globifer* and a single individual of *H. gurdus*, *H. gredensis* and *H. ravastellus*, respectively. The *16S-nadl* fragment was amplified with primer pairs LR-N-13398 (Simon et al. 1994) and N1-J-12350 (5′-CCTARTTGRCTAR-ARTTRGCRSATCARCCAATTG -3′) and the *srp54* with SRP54fl

Table 2.—Overall diversity measures and statistics estimated across 15 anonymous loci, *srp54* intron and *16s-nad1* mitochondrial fragment for *Harpactocrates globifer*. Sample size (SS) indicates the number of individuals sequenced for each locus, in brackets the number of individuals used in the estimations considering the 0.9 probability threshold in PHASE. The length (L) in bp for each locus after sequences end-trimming and excluding sites with gaps. The lengths of indels are indicated as they occurred in each locus (N/A: not applicable, if indels were not observed). The number of segregating sites (S) and haplotypes (H), nucleotide diversity (π), minimum number of recombination events (R_M) of Hudson (1985), linkage disequilibrium statistic (ZZ) of Rozas et al. (2001), Tajima's D test (D) of Tajima (1989), and the HKA test of Hudson (1987). Not significant (ns) and significant (*) values at $P < 0.05$ of statistics after coalescence simulations.

	H. globifer									HKA Test (*H. globifer*/*H. gredensis*) *srp54* vs. other locus
Locus	SS	L	Indel length	S	H	π	R_M	ZZ	D	
qgL1	10 (10)	313	N/A	8	3	0.0031	0	0.0000	−1.9072 *	$P = 0.4764$ ns
qgL5	10 (10)	342	N/A	5	4	0.0039	2 ns	0.0477 ns	−0.1917 ns	$P = 0.5292$ ns
qgL10	9 (6)	540	1, 8	12	7	0.0057	0	0.1707 ns	−0.9653 ns	$P = 0.7549$ ns
qgL12	8 (8)	542	1, 2	16	7	0.0071	0	0.2002 ns	−0.8083 ns	$P = 0.2500$ ns
qgL21	10 (9)	496	1, 2	15	10	0.0088	1 ns	0.1057 ns	−0.0070 ns	$P = 0.7649$ ns
qgL22	10(10)	429	3, 1, 2	16	5	0.0140	0	0.0360 ns	1.2410 ns	$P = 0.4838$ ns
qgL25	10 (9)	223	6, 1	1	2	0.0009	0	0.1170 ns	−0.5290 ns	$P = 0.2839$ ns
qgL26	10 (8)	512	N/A	2	3	0.0005	0	0.0000	−1.4979 *	$P = 0.3564$ ns
qgL28	10 (10)	317	N/A	8	6	0.0068	0	− 0.0570 ns	−0.1529 ns	$P = 0.4341$ ns
qgL29	10 (9)	373	N/A	12	6	0.0070	1 ns	0.1465 ns	−0.9463 ns	$P = 0.9255$ ns
qgL32	10 (9)	490	5, 11, 3, 10	21	5	0.0119	0	0.0665 ns	−0.1766 ns	$P = 0.5201$ ns
qgL33	10 (10)	266	N/A	12	7	0.0142	1 ns	−0.0074 ns	0.4320 ns	$P = 0.5290$ ns
qgL34	10 (10)	319	1	13	8	0.0108	0	0.0678 ns	−0.4578 ns	$P = 0.8684$ ns
qgL36	10 (8)	552	N/A	11	6	0.0057	0	−0.0444 ns	−0.1786 ns	$P = 0.5850$ ns
qgL38	10 (9)	366	N/A	5	3	0.0067	0	0.2154 ns	2.1431 ns	$P = 0.3583$ ns
srp54	10 (10)	119	N/A	7	8	0.0165	1 ns	−0.0154 ns	−0.0165 ns	-
16S-nad1	10 (10)	851	1	76	9	0.0237	7 ns	−0.0103 ns	−1.5465 ns	$P = 0.1021$ ns

and SRP52r1 (Jarman et al. 2002). PCR conditions were as follows: 94° C for 2 min; 35× (94° C for 35 s; 45° C for 45 s for *16S-nad1* and from 45° C to 50° C for 35 s for *srp54*; 72° C for 45 s for *16S-nad1* and 35 s for *srp54*; 72° C for 5 min).

The allelic phase of heterozygotic individuals was resolved using the algorithms provided by PHASE (Stephens et al. 2001; Stephens & Donnelly 2003) and implemented in DnaSP v5 (Librado & Rozas 2009). In the case where direct sequencing detected multiple copies of different lengths, either as a result of heterozygote individuals or paralogy, the PCR products were cloned and four to eight colonies sequenced. Cloning results were compatible with alleles of different length (i.e., high sequence similarity) rather than paralogous copies, assuming that polymorphisms due to singleton mutations among sequenced colonies represented errors of the *Taq* polymerase enzyme or cloning artifacts (see Villablanca et al. 1998; Calderón et al. 2009; Cummings et al. 2010; Dawson et al. 2010).

The taxonomic range of applicability of the novel markers was evaluated by screening a sample of specimens belonging to groups at different hierarchical levels: *Parachtes romandiolae* Caporiacco 1949 and *Dysdera erythrina* Walckenaer 1802 (Araneomorphae, Haplogynae, Dysderidae, Dysderinae), *Harpactea corticalis* Simon 1882 (Araneomorphae, Haplogynae, Dysderidae, Harpacteinae), *Loxosceles rufescens* Dufour 1820 (Araneomorphae, Haplogynae, Sicariidae), *Troglohyphantes lucifuga* Simon 1884 and *T. pedemontanus* Gozo 1908 (Araneomorphae, Entelegynae, Linyphiidae), and *Nemesia randa* Decae 2005 and *Iberesia brami* L. Koch 1882 (Mygalomorphae, Nemesiidae). Two independent PCR amplifications were performed for each locus using the following touchdown cycle: 94° C 2 min; 10× [94° C for 35 s, 63° C for 35 s (−0.5° C/cycle), 72° C for 1 min]; 10× [94° C for 35 s, 58° C for 35 s, 72° C for 1 min]; 15× [94° C for 35 s, 52° C for 35 s, 72° C for 1 min]; 72° C for 10 min. Results of the amplification success are summarized in Table 1.

The average interspecific sequence divergence (*p* distance) of the anonymous loci calculated with DnaSP v5 ranged from 0.02% (qgL26) to 8.1% (qgL28) between *H. globifer* and *H. gurdus*, 0.41% (qgL26) to 6.9% (qgL33) between *H. globifer* and *H. gredensis*, 1.8% (qgL25) to 11.1% (qgL1) between *H. globifer* and *H. ravastellus*, 0.39% (qgL26) to 8.5% (qgL28) between *H. gurdus* and *H. gredensis*, 1.3% (qgL25) to 13.9% (qgL28) between *H. gurdus* and *H. ravastellus*, and 2.4% (qgL25) to 9.4% (qgL1) between *H. gredensis* and *H. ravastellus*. Percent nucleotide diversity within *H. globifer* ranged from 0.05% (qgL26) to 1.4% (qgL33). Genetic diversity indices, recombination and linkage disequilibrium measures and neutrality tests were calculated for each locus in *H. globifer* using DnaSP v5. Results are summarized in Table 2. We applied the HKA test of Hudson (1987) to assess whether levels of polymorphism and divergence were correlated, as predicted by neutral theory. The test was performed by comparing polymorphism in *H. globifer* and divergence between *H. globifer* and *H. gredensis* in the intron *srp54* versus each of the 15 anonymous loci and versus the mitochondrial fragment *16s-nad1*. Neither recombination nor linkage disequilibrium were found at any locus. None of the HKA tests showed deviation from neutral predictions, although Tajima's D test showed significant negative values for the loci qgL1 and qgL26. The mitochondrial fragment *16S-nad1* was 1.4 times more variable than the intron *srp54*, and from 1.7 to 47 times more variable than the anonymous loci qgL33 and qgL26, which are the most and least variable ANM's, respectively.

This study reports the first ANMs ever designed specifically for spiders. These kinds of markers, however, have been isolated and extensively applied in other organisms; e.g., grasshoppers (Carstens & Knowles 2006), halfbeaks and killifishes (De Bruyn et al. 2010a, b), oysters (Hare et al. 1996), birds (Lee & Edwards 2008) and lizards (Rosenblum et al. 2007; Noonan & Yoder 2009). ANMs are promising markers for multilocus approaches at the population and species level of closely related and recently diverged species, as has been shown in recent studies (Carstens & Knowles 2007a; Carstens & Richards 2007; Knowles et al. 2007; Lee & Edwards 2008). The novel ANMs designed here are potentially useful not only for the target species, but also for more distantly related species in the genus (e.g., *H. ravastellus*), as well as for species in related genera (e.g. *Parachtes*), or even subfamilies (e.g., *Dysdera*, see Table 1). However, the

applicability of these novel markers is compromised at higher taxonomic levels. A significant and negative relationship between performance and evolutionary distance from the target species is also observed among the popular microsatellite markers (Primmer et al. 1996). Although the strategy implemented in our study greatly facilitates and speeds up the isolation of variable markers for populations and species, the advent of the so-called next-generation sequencing (NGS) methods promise to revolutionize the discovery of novel markers in non-model organism even further. In fact, the protocols used here for ANM isolation can be easily coupled with NGS methods, simply by replacing the cloning step, to generate literally hundreds or thousands of novel markers for spiders. Moreover, NGS allows sequencing of lots of markers from multiple individuals and populations simultaneously. No doubt NGS methods will spawn a whole new era for phylogenetic, phylogeographic and population genetic studies in spiders and their allies.

ACKNOWLEDGMENTS

We are grateful to J. Pons for his invaluable technical advice. We also thank P. Croucher and A. Lam for their assistance in the lab. The project was funded by the Spanish Ministry of Science and Innovation (MICINN) grant CGL2006-08617 (MA) and the William and Esther Schlinger Chair in Systematic Entomology (RGG). LBB was supported by a graduate grant (FI-DGR 2009) and a short stay grant (BE 2009) from the Generalitat de Catalunya. Further funding support was provided by an ICREA Academia award for excellence in research from the Generalitat de Catalunya to MA.

LITERATURE CITED

Avise, J.C. 2000. Phylogeography: the History and Formation of Species. Harvard University Press, Cambridge, Massachusetts.

Ayoub, N.A., J.E. Garb, M. Hedin & C.Y. Hayashi. 2007. Utility of the nuclear protein-coding gene, elongation factor-1 gamma (EF-1γ), for spider systematics, emphasizing family level relationships of tarantulas and their kin (Araneae: Mygalomorphae). Molecular Phylogenetics and Evolution 42:394–409.

Ballard, J.W.O. & M.C. Whitlock. 2004. The incomplete natural history of mitochondria. Molecular Ecology 13:729–744.

Bidegaray-Batista, L., N. Macías-Hernández, P. Oromí & M.A. Arnedo. 2007. Living on the edge: demographic and phylogeographical patterns in the woodlouse-hunter spider *Dysdera lancerotensis* Simon, 1907 on the eastern volcanic ridge of the Canary Islands. Molecular Ecology 16:3198–3214.

Bond, J.E. & A.K. Stockman. 2008. An integrative method for delimiting cohesion species: finding the population-species interface in a group of Californian trapdoor spiders with extreme genetic divergence and geographic structuring. Systematic Biology 57:628–646.

Brito, P.H. & S.V. Edwards. 2009. Multilocus phylogeography and phylogenetics using sequence-based markers. Genetica 135:439–455.

Brumfield, R.T., P. Beerli, D.A. Nickerson & S.V. Edwards. 2003. The utility of single nucleotide polymorphisms in inferences of population history. Trends in Ecology & Evolution 18:249–256.

Calderón, I., X. Turon & H.A. Lessios. 2009. Characterization of the sperm molecule bindin in the sea urchin genus *Paracentrotus*. Journal of Molecular Evolution 68:366–376.

Carstens, B.C. & L.L. Knowles. 2006. Variable nuclear markers for *Melanoplus oregonensis* identified from the screening of a genomic library. Molecular Ecology Notes 6:683–685.

Carstens, B.C. & L.L. Knowles. 2007a. Estimating species phylogeny from gene-tree probabilities despite incomplete lineage sorting: an example from *Melanoplus* grasshoppers. Systematic Biology 56:400–411.

Carstens, B.C. & L.L. Knowles. 2007b. Shifting distributions and speciation: species divergence during rapid climate change. Molecular Ecology 16:619–628.

Carstens, B.C. & C.L. Richards. 2007. Integrating coalescent and ecological niche modeling in comparative phylogeography. Evolution 61:1439–1454.

Cummings, S.M., M. McMullan, D.A. Joyce & C. Van Oosterhout. 2010. Solutions for PCR, cloning and sequencing errors in population genetic analysis. Conservation Genetics 11:1095–1097.

Dawson, K., R.S. Thorpe, A. Malhotra & T. Mailund. 2010. Estimating genetic variability in non-model taxa: a general procedure for discriminating sequence errors from actual variation. PLoS One 5:551–554.

De Bruyn, M., W. Grail, A. Barlow & G.R. Carvalho. 2010a. Anonymous nuclear markers for SouthEast Asian halfbeak fishes (*Dermogenys*). Conservation Genetics Resources 2:325–327.

De Bruyn, M., W. Grail & G.R. Carvalho. 2010b. Anonymous nuclear markers for the Blue Panchax killifish (*Aplocheilus panchax*). Conservation Genetics Resources 3:53–55.

De Busschere, C., F. Hendrickx, S.M. Van Belleghem, T. Backeljau, L. Lens & L. Baert. 2010. Parallel habitat specialization within the wolf spider genus *Hogna* from the Galápagos. Molecular Ecology 19:4029–4045.

DeChaine, E.G. & A.P. Martin. 2005. Marked genetic divergence among sky island populations of *Sedum lanceolatum* (Crassulaceae) in the Rocky Mountains. American Journal of Botany 92:477–486.

Edwards, S.V. 2009. Is a new and general theory of molecular systematics emerging? Evolution 63:1–19.

Ekblom, R. & J. Galindo. 2011. Applications of next generation sequencing in molecular ecology of non-model organisms. Heredity 107:1–15.

Garb, J.E. & R.G. Gillespie. 2009. Diversity despite dispersal: colonization history and phylogeography of Hawaiian crab spiders inferred from multilocus genetic data. Molecular Ecology 18:1746–1764.

Hare, M.P., S.A. Karl & J.C. Avise. 1996. Anonymous nuclear DNA markers in the American oyster and their implications for the heterozygote deficiency phenomenon in marine bivalves. Molecular Biology and Evolution 13:334.

Hare, M.P. 2001. Prospects for nuclear gene phylogeography. Trends in Ecology and Evolution 16:700–706.

Hedin, M.C. 1997. Molecular phylogenetics at the population/species interface in cave spiders of the Southern Appalachians (Araneae: Nesticidae: *Nesticus*). Molecular Biology and Evolution 14: 309–324.

Heled, J. & A.J. Drummond. 2010. Bayesian inference of species trees from multilocus data. Molecular Biology and Evolution 27:570–580.

Hey, J. & R. Nielsen. 2007. Integration within the Felsenstein equation for improved Markov chain Monte Carlo methods in population genetics. Proceedings of the National Academy of Sciences USA 104:2785–2790.

Hey, J. 2010. Isolation with migration models for more than two populations. Molecular Biology and Evolution 27:905–920.

Hudson, M.E. 2007. Sequencing breakthroughs for genomic ecology and evolutionary biology. Molecular Ecology Resources 8:3–17.

Hudson, R.R. & N.L. Kaplan. 1985. Statistical properties of the number of recombination events in the history of a sample of DNA sequences. Genetics 111:147–164.

Hudson, R.R., M. Kreitman & M. Aguadé. 1987. A test of neutral molecular evolution based on nucleotide data. Genetics 116:153–159.

Irwin, D.E. 2002. Phylogeographic breaks without geographic barriers to gene flow. Evolution 56:2383–2394.

Jarman, S.N., R.D. Ward & N.G. Elliott. 2002. Oligonucleotide primers for PCR amplification of coelomate introns. Marine Biotechnology 4:347–355.

Knowles, L.L. 2001. Did the Pleistocene glaciations promote divergence? Tests of explicit refugial models in montane grasshoppers. Molecular Ecology 10:691–702.

Knowles, L.L., B.C. Carstens & P. Sunnucks. 2007. Estimating a geographically explicit model of population divergence. Evolution 61:477–493.

Kuo, C.H. & J.C. Avise. 2005. Phylogeographic breaks in low-dispersal species: the emergence of concordance across gene trees. Genetica 124:179–186.

Lee, J.Y. & S.V. Edwards. 2008. Divergence across Australia's Carpentarian barrier: statistical phylogeography of the red-backed fairy wren (*Malurus melanocephalus*). Evolution 62:3117–3134.

Librado, P. & J. Rozas. 2009. DnaSP v5: a software for comprehensive analysis of DNA polymorphism data. Bioinformatics 25:1451–1452.

Maddison, W. & M. Hedin. 2003. Phylogeny of *Habronattus* jumping spiders (Araneae: Salticidae), with consideration of genital and courtship evolution. Systematic Entomology 28:1–22.

Maddison, W.P. 1997. Gene trees in species trees. Systematic Biology 46:523–536.

Mardulyn, P., Y.E. Mikhailov & J.M. Pasteels. 2009. Testing phylogeographic hypotheses in a Euro-Siberian cold-adapted leaf beetle with coalescent simulations. Evolution 63:2717–2729.

Masta, S.E. 2000. Phylogeography of the jumping spider *Habronattus pugillis* (Araneae: Salticidae): recent vicariance of sky island populations? Evolution 54:1699–1711.

Muster, C., W.P. Maddison, S. Uhlmann, T.U. Berendonk & A.P. Vogler. 2009. Arctic-alpine distributions-metapopulations on a continental scale? American Naturalist 173:313–326.

Noonan, B.P. & A.D. Yoder. 2009. Anonymous nuclear markers for Malagasy plated lizards (*Zonosaurus*). Molecular Ecology Resources 9:402–404.

Primmer, C.R., A.P. Møller & H. Ellegren. 1996. A wide range survey of cross species microsatellite amplification in birds. Molecular Ecology 5:365–378.

Rosenblum, E.B., N.M. Belfiore & C. Moritz. 2007. Anonymous nuclear markers for the eastern fence lizard, *Sceloporus undulatus*. Molecular Ecology Notes 7:113–116.

Rozas, J., M. Gullaud, G. Blandin & M. Aguade. 2001. DNA variation at the rp49 gene region of *Drosophila simulans*: evolutionary inferences from an unusual haplotype structure. Genetics 158:1147–1155.

Schmitt, T. 2009. Biogeographical and evolutionary importance of the European high mountain systems. Frontiers in Zoology 6:1–10.

Simon, C., F. Frati, A. Beckenbach, B. Crespi, H. Liu & P. Flook. 1994. Evolution, weighting, and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction primers. Annals of the Entomological Society of America 87:651–701.

Stephens, M., N.J. Smith & P. Donnelly. 2001. A new statistical method for haplotype reconstruction from population data. American Journal of Human Genetics 68:978–989.

Stephens, M. & P. Donnelly. 2003. A comparison of bayesian methods for haplotype reconstruction from population genotype data. American Journal of Human Genetics 73:1162–1169.

Tajima, F. 1989. Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. Genetics 123:585–595.

Thomson, R.C., I.J. Wang & J.R. Johnson. 2010. Genome enabled development of DNA markers for ecology, evolution and conservation. Molecular Ecology 19:2184–2195.

Villablanca, F.X., G.K. Roderick & S.R. Palumbi. 1998. Invasion genetics of the Mediterranean fruit fly: variation in multiple nuclear introns. Molecular Ecology 7:547–560.

Vink, C.J., M. Hedin, M.R. Bodner, W.P. Maddison, C.Y. Hayashi & J.E. Garb. 2008. Actin 5C, a promising nuclear gene for spider phylogenetics. Molecular Phylogenetics and Evolution 48:377–382.

Wilkins, J.F. 2004. A separation-of-timescales approach to the coalescent in a continuous population. Genetics 168:2227–2244.

Yang, Z. & B. Rannala. 2010. Bayesian species delimitation using multilocus sequence data. Proceedings of the National Academy of Sciences USA 107:9264–9269.

Manuscript received 25 June 2011, revised 27 September 2011.

2011. The Journal of Arachnology 39:511–514

SHORT COMMUNICATION

Nesticus eremita (Araneae: Nesticidae): redescription of a potentially invasive European spider found in New Zealand

Cor J. Vink[1,2] and **Nadine Dupérré**[3]: [1]Biosecurity Group, AgResearch, Private Bag 4749, Christchurch 8140, New Zealand. E-mail: cor.vink@agresearch.co.nz; [2]Entomology Research Museum, PO Box 84, Lincoln University, Lincoln 7647, New Zealand; [3]Division of Invertebrate Zoology, American Museum of Natural History, Central Park West at 79th Street, New York, NewYork 10024 USA

Abstract. *Nesticus eremita* Simon 1879 is naturally found in caves in southern Europe. It has also invaded and established itself in Germany and has now been found in an abandoned air-raid tunnel in Auckland, New Zealand. A diagnosis, redescription, full synonymy and illustrations are presented to aid in the identification of this potentially invasive spider.

Keywords: Cave spider, invasive species, taxonomy, troglophile

A number of species in the family Nesticidae have invaded areas outside their natural range. *Nesticus cellulanus* (Clerck 1757) is originally from Europe, but is now found in the northeastern USA and Québec (Gertsch 1984; Paquin & Dupérré 2003; Paquin & Hedin 2005). *Eidmanella pallida* (Emerton 1875) was originally from North and Central America (Gertsch 1984), but is now found throughout the world (Platnick 2011). *Nesticella mogera* (Yaginuma 1972), is native to Asia but introduced to Fiji, Germany and Hawaii (Lehtinen & Saaristo 1980; Gertsch 1984; Kielhorn 2009).

Here we document another nesticid that has spread outside its natural range. *Nesticus eremita* Simon 1879 occurs naturally in caves throughout Italy, southeast France, Corsica, Switzerland, Slovenia, Croatia, Montenegro, Bosnia-Herzegovina and Greece (Lessert 1906, 1910; Kratochvíl 1933; Dresco 1966; Dresco & Hubert 1967; Brignoli 1971, 1977; Deeleman-Reinhold 1974; Maurer & Hänggi 1990). It is also found in cave-like synanthropic habitats (e.g., tunnels, cellars, catacombs, railroad track ballast, wells) in its natural range (Brignoli 1971; Maurer & Hänggi 1990) and where it is adventive in Austria (Knoflach & Thaler 1998) and Germany (Jäger 1995, 1998; Staudt 2010). *Nesticus eremita* has established populations in sewer tunnels in the German cities of Cologne, Mainz and Mannheim (Jäger 1995, 1998). These cites are all on the Rhine River, and *N. eremita* may have spread downstream from its endemic range in the Alps either naturally or via human transport (Jäger 1998). Given that the sewer tunnels in which *N. eremita* was found were not much more than 100 years old (Jäger 1995, 1998) and that the spider fauna of Central Europe is well known (e.g., Heimer & Nentwig 1991), it appears that *N. eremita* has become established in Germany comparatively recently.

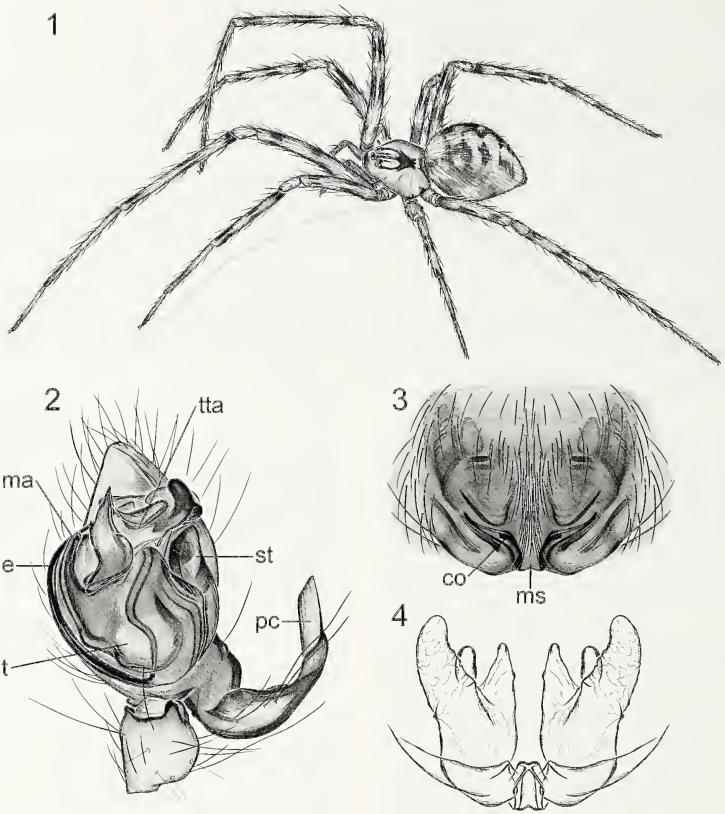
On 21 June 2000, CJV and Grace Hall went to an abandoned air-raid tunnel in Alten Reserve (36°51.04′S, 174°46.42′E) in central Auckland in search of the Australian stiphidiid *Procambridgea grayi* Davies 2001, which had been collected from there in 1999 (Davies & Lambkin 2001). No specimens of *P. grayi* were found, but a single male *N. eremita* was collected from a web near the entrance of the tunnel. Neither collector recognized the specimen as belonging to Nesticidae, as that family had not been recorded from New Zealand (Paquin et al. 2010; Sirvid, et al. 2011). The specimen was preserved in 70% EtOH, labeled and put amongst the unsorted material at the New Zealand Arthropod Collection (NZAC); it remained there until November 2010 when CJV noticed it while searching for specimens of Mimetidae.

It seems almost certain that *N. eremita* arrived in Auckland via a shipping container, as the tunnel entrance in Alten Reserve is only 600 meters from the Port of Auckland, which is one of New Zealand's busiest seaports. The air-raid tunnels beneath Albert Park in Auckland city are extensive and were partially filled with unfired bricks at the end of the Second World War, when most of the entrances were blocked off (Pilkington 2008).

The male specimen collected had built a web and was in good condition. It would be extremely unlikely that the single male collected had lived long enough to stow away with cargo, made the journey from Europe to New Zealand (it takes about 40 days for a cargo ship to sail from Italy to Auckland (M.R. McNeill pers. comm.)), walked the 600 m from the port to the tunnel and then made a web. It is more likely that the male was part of an established population or, at the very least, the offspring of a gravid female that did live long enough to make the journey from Europe. The establishment of *N. eremita* in Auckland needs further confirmation. Unfortunately, the entrance to the tunnel where the single male specimen of *N. eremita* was collected in 2000 has since been blocked off, so it was not possible to search for further specimens and confirm whether there is still a population there.

Given that people generally do not spend a great deal of time looking for small spiders in sewers and abandoned tunnels, it is quite possible that *N. eremita* has spread to other parts of the world and established undetected populations. The presence of *N. eremita* in human-made tunnels in Auckland, Cologne, Mainz and Mannheim does not present an immediate threat to natural ecosystems. However, if this species were to spread to natural cave systems outside its native range, it has the potential for making ecological impacts. Invasive spider species can harm endemic spiders through competitive displacement (Nyffeler et al. 1986; Hann 1990; Bednarski et al. 2010), and invasive arthropod predators can impact native communities (Snyder & Evans 2006). This may be even more of a concern in cave ecosystems, which may be more at risk from ecological disturbance (Reeves 2001).

The species descriptions of *N. eremita* are all in relatively inaccessible publications, not in English or do not feature diagnostic illustrations of male and female genitalia together. To facilitate the identification of this potentially invasive species we present a full synonymy, diagnosis, brief redescription and illustrations of the habitus, male pedipalp and female epigynum. Terminology of the male pedipalpal structures follows Agnarsson et al. (2007).



Figures 1–4.—*Nesticus eremita*, female from Mannheim, male from Mainz, Germany. 1. Habitus, female; 2. Male left pedipalp, ventral view, tta = theridioid tegular apophysis, e = embolus, ma = median apophysis, t = tegulum, st = subtegulum, pc = paracymbium; 3. External genitalia, ventral view, co = copulatory opening, ms = medium septum; 4. Internal genitalia, dorsal view.

TAXONOMY

Nesticidae Simon 1894
Nesticinae Simon 1894
Nesticus Thorell 1869
Nesticus eremita Simon 1879
(Figs. 1–4)

Nesticus eremita Simon 1879:258; Simon 188:48, pl. 26, fig. 8; Lessert 1906:610, pl. 20, figs. 3–5; Lessert 1910:300, figs. 164–166; Simon 1929:658, 753, figs. 1015, 1016; Dresco 1966:805; Dresco & Hubert 1967:3; Brignoli 1971:206, figs. 118–122; Deeleman-Reinhold 1974:12, fig. 9; Brignoli 1975:28; Kratochvíl 1978:39, figs. 3, 4; Thaler 1981:274, figs. 6, 8; Heimer & Nentwig 1991:276, fig. 732; Jäger 1998:13, fig. 1A.

Theridion parenzani Trossarelli 1931:13, fig. 1 (Synonymized by Brignoli 1975);

Nesticus strasseri Roewer 1931:14, fig. 11, 13c, d (Synonymized by Kratochvíl 1933).

Nesticus eremita italica Caporiacco 1934:401, figs. 2, 3 (Synonymized by Dresco & Hubert 1967).

Nesticus speluncarum eremita Kratochvíl 1933:40, 63, figs. 3, 13, 14, 27–30; Wiehle 1963:435, figs. 8–10; Wiehle 1967:193, figs. 45, 46 (Synonymized by Dresco & Hubert 1967).

Ivesia eremita Lehtinen & Saaristo 1980:51 (Transferred from *Nesticus*).

Material examined.—NEW ZEALAND: Auckland, Alten Reserve, 21 June 2000, C.J. Vink & G. Hall leg, 1♂ (NZAC). GERMANY: Mannheim, 24 November 1997, P. Jäger leg. 1♂ 1♀ (AMNH); Mainz, 21 May 1996, P. Jäger leg. 1♂ 1♀ (AMNH).

Diagnosis.—*Nesticus eremita* can be distinguished from other Nesticidae by features of the male pedipalp (Fig. 2), particularly the structure of the theridioid tegular apophysis, the shape of the large, unbranched paracymbium and the structure of the external genitalia of the female (Fig. 3). The theridioid tegular apophysis is more compact than that of *N. celludanus*, and the distal end of the paracymbium is rounded. The slit-like copulatory openings of the

external genitalia diverge anteriorly and the medium septum narrows posteriorly, whereas in *N. cellulanus*, the copulatory openings converge anteriorly, and the medium septum is wide posteriorly.

Redescription.—Color in alcohol: Male carapace light yellow; abdomen off-white; legs yellow, metatarsi, tarsi of legs I, II light orange. Female carapace light yellow with black trident-shaped mark extending from fovea to lateral eyes (Fig. 1); abdomen off-white with dark pattern (Fig. 1); legs yellow-orange with dark bands (Fig. 1).

Male pedipalp (Fig. 2): theridioid tegular apophysis compact, with several pointed projections; paracymbium long, unbranched with rounded end. Male chelicerae with 3 promarginal teeth, 5 retromarginal denticles.

Epigynum (Fig. 3) with slit-like copulatory openings that diverge anteriorly, medium septum narrow posteriorly; internal genitalia (Fig. 4) with branched spermathecae. Female chelicerae with 3 promarginal teeth, 10 retromarginal denticles.

Dimensions (mm). Male (Auckland): total length 3.5; carapace length 1.9, width 1.8, height 0.8; abdomen length 2.6, width 1.4; sternum length 1.1, width 1.1; total length of leg I 16.7, leg II 11.7, leg III 8.7, leg IV 11.9. Female (Mainz): total length 5.2; carapace length 2.1, width 1.7, height 0.9; abdomen length 3.3, width 2.3; sternum length, 1.1, width 1.1; total length of leg I 15.8, leg II 10.9, leg III 7.7, leg IV 11.2.

Variation.—Female: Carapace length 1.7–2.6; total length 3.8–5.4. Male: Carapace length 1.7–2.3; total length 3.5–4.7. Based on material examined and Jäger (1998). The degree of pigmentation in *N. eremita* can vary (Jäger 1998); we observed uniformly light colored specimens and specimens with a contrasting color pattern on the abdomen and legs (Fig. 1).

Distribution.—*Nesticus eremita* is found in caves in its natural range throughout Italy, southeast France, Corsica, Switzerland, Slovenia, Croatia, Montenegro, Bosnia-Herzegovina and Greece. It has also been found in synanthropic habitats (e.g., tunnels, cellars, catacombs, railroad track ballast, wells) in Italy, Switzerland, Austria, Germany and New Zealand (Auckland).

Biology.—Like most nesticids, *Nesticus eremita* is a troglophile. Specimens of *N. eremita* that live well away from sunlight have less somatic pigmentation and reduced tapeta (Jäger 1998).

DNA sequences.—DNA sequences from the mitochondrial genes cytochrome *c* oxidase subunit 1 (COI) (GenBank accession number EU746436) and 16S ribosomal RNA (EU746445) were reported in López-Pancorbo & Ribera (2011).

Remarks.—The position of the trichobothrium on metatarsus 1 has been promoted as an important character for distinguishing between *N. eremita* and *N. cellulanus* (Wiehle 1963; Thaler 1981; Heimer & Nentwig 1991) and for higher nesticid taxonomy (Lehtinen & Saaristo 1980); however, Jäger (1998) found that this character was not diagnostic between *N. eremita* and *N. cellulanus*. Lehtinen & Saaristo (1980) transferred *Nesticus eremita* to the genus *Ivesia* Petrunkevitch 1925, but Kaston (1945) and Gertsch (1984) considered *Nesticus* a senior synonym of *Ivesia*. The pedipalpal sclerites of *N. eremita* are similar to those of *N. cellulanus*, the type species of *Nesticus*, and appear to be homologus. These two species also appear to be closely related based on a phylogenetic analysis of mitochondrial DNA (López-Pancorbo & Ribera 2011). There are European *Nesticus* species with greater morphological similarities to *N. eremita* (e.g., *N. speluncarum* Pavesi 1873, *N. henderickxi* Bosselaers 1998), but unlike *N. cellulanus*, these species are only known from their natural cave habitats and have limited distributions (Dresco 1966; Brignoli 1971; Bosselaers 1998).

ACKNOWLEDGMENTS

Grace Hall is always an excellent host when visiting the New Zealand Arthropod Collection. Peter Jäger (Senckenberg Museum) kindly gifted specimens of *N. eremita* to AMNH for us to study and he and Theo Blick (Senckenberg Museum) provided information about German localities. Thanks to Mark McNeill for providing information on times taken by cargo ships to reach Auckland. We thank Norman Platnick (American Museum of Natural History), Ingi Agnarsson (University of Puerto Rico) and two anonymous reviewers for comments on the manuscript. CJV was partially funded by New Zealand's Foundation for Research, Science and Technology through contracts C02X0501 (Better Border Biosecurity (B3) programme (www.b3nz.org)) and C09X0501 (Defining New Zealand's Land Biota / Te Tautuhi i ngā Hanga Koiora o Aotearoa).

LITERATURE CITED

Agnarsson, I., J.A. Coddington & B. Knoflach. 2007. Morphology and evolution of cobweb spider male genitalia (Araneae, Theridiidae). Journal of Arachnology 35:334–395.

Bednarski, J., H. Ginsberg & E.M. Jakob. 2010. Competitive interactions between a native spider (*Frontinella communis*, Araneae: Linyphiidae) and an invasive spider (*Linyphia triangularis*, Araneae: Linyphiidae). Biological Invasions 12:905–912.

Bosselaers, J. 1998. *Nesticus henderickxi* (Araneae, Nesticidae), a new blind troglobitic spider from Crete. Bulletin of the British Arachnological Society 11:9–14.

Brignoli, P.M. 1971. Note su ragni cavernicoli italiani (Araneae). Fragmenta Entomologica 7:121–229.

Brignoli, P.M. 1975. Ragni d'Italia. XXV. Su alcuni ragni cavernicoli dell'Italia settentrionale (Araneae). Notiziario del Circolo Speleologico Romano 20:7–39.

Brignoli, P.M. 1977. Ragni de Grecia X. Nuovi dati sulla Grecia continentale ed insulare (Araneae). Revue Suisse de Zoologie 84:937–954.

Caporiacco, L. 1934. I *Nesticus* liguri ed emiliani. Annali del Museo Civico di Storia Naturale di Genova 56:395–405.

Davies, V.T. & C.L. Lambkin. 2001. A revision of *Procambridgea* Fortser & Wilton, (Araneae: Amaurobiodea: Stiphidiidae). Memoirs of the Queensland Museum 46:443–459.

Deeleman-Reinhold, C.L. 1974. The cave spider fauna of Montenegro (Araneae). Glasnik Republickog Zavoda za Zastitu Prirode i Prirodnjackog Muzeja Titogradu 6:9–33.

Dresco, E. 1966. Étude de quelques espèces d'araignées du genre Nesticus (fam. Nesticidae). Annales de Spéléologie 21:795–813.

Dresco, E. & M. Hubert. 1967. Étude des variations oculaires chez Nesticus eremita Simon (Araneae, Nesticidae). Archives de Zoologie Expérimentale et Générale 108:3–31.

Gertsch, W.J. 1984. The spider family Nesticidae (Araneae) in North America, Central America, and the West Indies. Bulletin of the Texas Memorial Museum 31:1–91.

Hann, S.W. 1990. Evidence for the displacement of an endemic New Zealand spider, *Latrodectus katipo* Powell by the South African species *Steatoda capensis* Hann (Araneae: Theridiidae). New Zealand Journal of Zoology 17:295–308.

Heimer, S. & W. Nentwig. 1991. Spinnen Mitteleuropas: Ein Bestimmungsbuch. Paul Parey, Berlin.

Jäger, P. 1995. Erstnachweis von *Holocnemus pluchei* und zweiter Nachweis von *Nesticus eremita* für Deutschland in Köln (Araneae: Pholcidae, Nesticidae). Arachnologische Mitteilungen 10:23–24.

Jäger, P. 1998. Weitere Funde von *Nesticus eremita* (Araneae: Nesticidae) in Süddeutschland mit Angaben zur Taxonomie im Vergleich zu *N. cellulanus*. Arachnologische Mitteilungen 15:13–20.

Kaston, B.J. 1945. New Micryphantidae and Dictynidae with notes on other spiders. American Museum Novitates 1292:1–14.

Kielhorn, K.-H. 2009. First records of *Spermophora kerinci*, *Nesticella mogera* and *Pseudanapis aloha* on the European mainland (Araneae: Pholcidae, Nesticidae, Anapidae). Arachnologische Mitteilungen 37:31–34.

Knoflach, B. & K. Thaler. 1998. Kugelspinnen und verwandte Familien von Österreich: Ökofaunistische Übersicht (Araneae: Theridiidae, Anapidae, Mysmenidae, Nesticidae). Stapfia 55:667–712.

Kratochvíl, J. 1933. Evropské druhy čeledi *Nesticidae* Dahl. Práce Moravské Přírodovědecké Společnosti 8(10):1–69.

Kratochvíl, J. 1978. Araignées cavernicoles des îles Dalmates. Přírodovědné Práce Ústavů Československé Akademie věd v Brně 12(4):1–59.

Lehtinen, P.T. & M.I. Saaristo. 1980. Spiders of the Oriental-Australian region. II. Nesticidae. Annales Zoologica Fennici 17:47–66.

Lessert, R. 1906. Araneae. *In* Carl, J., Beitrag zur Höhlenfauna der insubrischen Region. Revue Suisse de Zoologie 14:601–615.

Lessert, R. 1910. Catalogue des invertebres de la Suisse. Fasc. 3, Araignées. Musée d'histoire naturelle de Genève, Geneva.

López-Pancorbo, A. & C. Ribera. 2011. *Nesticus baeticus* sp. n., a new troglobitic spider species from south-west Europe (Araneae, Nesticidae). ZooKeys 89:1–13.

Maurer, R. & A. Hänggi. 1990. Katalog der schweizerischen Spinnen. Documenta Faunistica Helvetiae, Neuchâtel, Switzerland.

Nyffeler, M., C.D. Dondale & J.H. Redner. 1986. Evidence for displacement of a North American spider, *Steatoda borealis* (Hentz), by the European species *S. bipunctata* (Linnaeus) (Araneae: Theridiidae). Canadian Journal of Zoology 64:867–874.

Paquin, P. & N. Dupérré. 2003. Guide d'identification des Araignées (Araneae) du Québec. Fabreries, Supplément 11:1–251.

Paquin, P. & M. Hedin. 2005. Nesticidae. Pp. 178–180. *In* Spiders of North America: An Identification Manual. (D. Ubick, P. Paquin, P.E. Cushing & V.D. Roth, eds.). American Arachnological Society, Keene, New Hampshire.

Paquin, P., C.J. Vink & N. Dupérré. 2010. Spiders of New Zealand: Annotated Family Key and Species List. Manaaki Whenua Press, Lincoln, New Zealand.

Pilkington, S. 2008. Heritage values of the Albert Park air raid shelters. Archaeology in New Zealand 51:106–117.

Platnick, N.I. 2011. The World Spider Catalog, version 11.5. American Museum of Natural History, New York. Online at http://research.amnh.org/entomology/spiders/catalog/INTRO1.html

Reeves, W.K. 2001. Exotic species in North American caves. Pp. 164–166. *In* Proceedings of the 1999 National Cave and Karst Management Symposium. (G.T. Rea, ed.). Southeastern Cave Conservancy, Chattanooga, Tennessee.

Roewer, C.F. 1931. Arachnoideen aus südostalpinen Höhlen gesammelt von Herrn Karl Strasser in den Jahren 1929 und 1930. Mitteilungen über Höhlen und Karstforschung 1931:1–17.

Simon, E. 1879. Arachnides nouveau de France, d'Espagne et d'Algérie. Premier mémoire. Bulletin de la Societe Zoologique de France 4:251–263.

Simon, E. 1881. Les Arachnides de France. Tome 5. 1ère partie contenant les families des Epeiridae (supplément) et des Theridionidae (commencement). Librairie encyclopédique de Roret, Paris.

Simon, E. 1929. Les Arachnides de France. Synopsis général et catalogue des espèces françaises de l'ordre des Araneae. Tome 6, 3e partie, Paris.

Sirvid, P.J., Z.-Q. Zhang, M.S. Harvey, B.E. Rhode, D.R. Cook, I. Bartsch & D.A. Staples. 2011. Chelicerata: horseshoe crabs, arachnids, sea spiders. Pp. 50–89. *In* New Zealand Inventory of Biodiversity. Volume Two: Kingdom Animalia—Chaetognatha, Ecdysozoa, Ichnofossils. (D.P. Gordon, ed.). Canterbury University Press, Christchurch, New Zealand.

Snyder, W.E. & E.W. Evans. 2006. Ecological effects of invasive arthropod generalist predators. Annual Review of Ecology, Evolution, and Systematics 37:95–122.

Staudt, A. 2010. Nachweiskarten der Spinnentiere Deutschlands (Arachnida: Araneae, Opiliones, Pseudoscorpiones). Deutsche Arachnologische Gesellschaft, online at http://www.spiderling.de/arages.

Thaler, K. 1981. Über *Nesticus idriacus* Roewer 1931 (Arachnida: Araneae: Nesticidae). Senckenbergiana Biologica 61:271–276.

Trossarelli, F. 1931. Aracnidi raccolti nella Grotta di Promontore (Istria). Atti dell'Accademia Scientifica Veneto-Trentino-Istriana 21:13–14.

Wiehle, H. 1963. Über *Nesticus borutzkyi* Reimoser (Arach., Araneae). Senckenbergiana Biologica 44:431–435.

Wiehle, H. 1967. *Meta*,-eine semientelegyne Gattung der Araneae (Arach.). Senckenbergiana Biologica 48:183–196.

Manuscript received 2 July 2011, revised 25 September 2011.

2011. The Journal of Arachnology 39:515–518

SHORT COMMUNICATION

Distribution of *Brachypelma vagans* (Theraphosidae) burrows and their characteristics in Belize over two years

Emma M. Shaw, Susan P. Bennett and **C. Philip Wheater**: Department of Environmental and Geographical Sciences, Manchester Metropolitan University, Manchester, M15 5GD, UK. E-mail: spideremma.shaw@gmail.com

Abstract. To help to address the paucity of ecological knowledge available for *Brachypelma vagans* Ausserer 1875, a CITES protected species, we monitored a population in Western Belize for two years to provide data for distribution and dispersal. Despite previous over-collection for the pet trade, the species is locally highly abundant in some areas of Belize. We recorded the distribution, burrow and spider characteristics of *B. vagans* in 2007 and 2008 at Las Cuevas Research Station, Belize. Population dynamics were compared between years, as was individual location. Over 100 burrows were located in both years; however, previous assumptions that individuals do not move burrows regularly appear negated, since only 12 burrow locations matched between years, suggesting high intra-habitat dispersal. Despite this apparent high level of movement burrows were significantly clumped, to a similar degree, in both years. This movement could be due to disturbances throughout the year, including flooding during the rainy season. Burrow size correlated with individual body size, except in a few juveniles that appear to have opportunistically claimed an empty burrow, accounting for some small animals found in large burrows.

Keywords: Burrow, Belize, ecology, red-rump tarantula, population structure

Brachypelma vagans Ausserer 1875 is one of the most ubiquitous *Brachypelma* species of Neotropical lowland forest habitats. As these tarantulas are long lived, brightly coloured, and usually docile, they are popular pets and suffer from over-harvesting, now being listed as threatened CITIES Appendix II species (Peterson et al. 2006). Despite *B. vagans* having the widest distribution of *Brachypelma* species (being recorded from Mexico, Belize and other parts of Central America: Reichling 1999), there is limited information on its ecology and habitat preferences (e.g., Yañez & Floater 2000; Hénaut & Machkour-M'Rabet 2005; Machkour-M'Rabet et al. 2007; Dor et al. 2008), with most studies on *Brachypelma* tarantulas concerning their geographic distributions (Valerio 1980; Smith 1986; Edwards & Hibbard 1999; Locht et al. 1999), systematics (Coddington & Levi 1991; Perez-Miles et al. 1996) and genetics (Longhorn 2002; Longhorn et al. 2007; Machkour-M'Rabet et al. 2009). The rarity of some *Brachypelma* species (e.g., Yañez & Floater 2000), combined with habitat degradation and illegal capture and trade, suggests the need for captive breeding prior to reintroduction (Yañez et al. 1999). It is essential therefore, to obtain detailed knowledge of their habitat requirements and changes within populations to provide a greater understanding of the factors influencing their spatial distribution and population dynamics.

Brachypelma vagans construct burrows with single entrances where they spend the day, spinning silk around the entrance to transmit vibrations from prey movements (Yañez & Floater 2000). They are nocturnal predators feeding mainly on ground-dwelling arthropods and possibly small vertebrates (Marshall 1996). Machkour-M'Rabet et al. (2007) found densities of *B. vagans* to be higher in open rather than forest sites and with high densities of burrows characterised by deep clayish soils, which is unsurprising given that individuals, on the whole, dig their own burrows. Little is known about burrow fidelity and which factors cause burrow relocation, although some field observations suggest that females locate occupied burrows of conspecifics and attack and consume the residents (Hénaut & Machkour-M'Rabet, 2005). Lack of long-term distributional data for any *B. vagans* population poses difficulties in determining the level of intra-population movement, whether burrow swapping occurs, or the distances that individuals move to find, or dig, a new burrow. The current study examines the population dynamics and distribution of one *B. vagans* population for two consecutive years to elucidate patterns of movement and activity and provide an understanding of the habitat requirements and population pressures on the species.

The techniques used over the two years were identical. The study site at Las Cuevas Research Station, Chiquibul rain forest area, Cayo district, Belize (GPS location 88°59.188′W, 16°43.990′N, elev. 583 m) is classified as lowland tropical broad-leafed rain forest, which stretches from the Caribbean coast of Mexico, through Belize and into Honduras and the Peten region of Guatemala. The study population of *B. vagans* is in the clearing (150 × 121 m) surrounding research station buildings, which are mainly to the south side (the current research concentrated on the north side of the clearing: 98 × 121 m). Belt transects (1 m wide) were laid perpendicular to the back of the clearing (where it met forest undergrowth) and systematically searched for signs of burrows, which were labelled using a numbered flag to enable easy relocation at night, when individuals were extracted for measurement. The location of each burrow and its opening dimensions (using the widest width and longest length of the mouth) were recorded. The surveys took place in June and July in both 2007 and 2008.

Visiting burrows at night when individuals sat at the burrow mouth gave a clear indication of occupaney and helped to minimize stress when removing animals using a fishing technique (Reichling 2003) involving a blade of grass waved to mimic prey movements. Once the individual was removed, the entrance was blocked and the individual placed in a clear plastic bag to allow manipulation and measurement. When individuals were not seen, the burrow was monitored for signs of occupancy (e.g., silk and soil extracted from the burrow).

The minimum distance between burrows was calculated using trigonometry, and aggregation between burrows was assessed using nearest neighbour analysis (e.g., Wheater et al. 2011). The index of aggregation was calculated as the ratio between the mean and the expected distances between burrows (where the expected distance was estimated as: $1/[2\sqrt{\text{density}}]$). Independent samples *t*-tests were used to examine differences in nearest neighbor distances between years to determine whether clustering differs between years (see Krebs 1999 for a fuller explanation of nearest neighbor analysis). A Pearson's

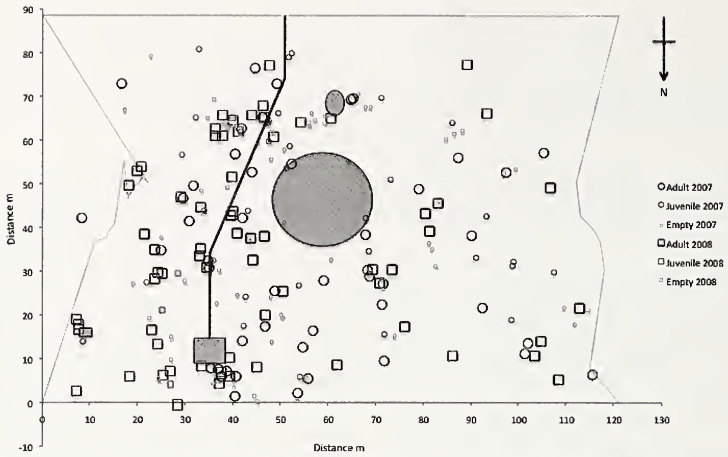


Figure 1.—Schematic representation of the location of all burrows located in 2007 and 2008 on the north side of the Las Cuevas Research Station clearing. The clearing boundaries, path and buildings and flood zone are all shown for reference (shaded areas).

product moment correlation coefficient was used to determine relationships between spider and burrow size, for all caught individuals, in each year.

Over 100 burrows were located (108 in 2007 and 107 in 2008), of which 80 were occupied in 2007, and 73 in 2008. More individuals were extracted in 2007 (48 compared to 26 in 2008), and there was a higher percentage of juveniles in 2007 (41%) than in 2008 (7%). Despite the similarity in burrow numbers found in both years, it is evident from Fig. 1 that their distribution is markedly different with only 12 present from 1 year to the next. Many burrows were located around buildings and on the edges of a concrete path. A large number of burrows were found in the west side of the clearing in 2007, whereas in 2008 the proportion present in this area was reduced. An area prone to flooding had few burrows present in either year (Fig. 1).

There was no significant difference between mean nearest neighbour distances between burrows in 2007 and 2008 ($t = 1.658$, df = 213, $P = 0.099$; 2007: mean = 3.88 (SE = 0.31) m; 2008: mean =3.16 (SE = 0.27) m). Burrows were significantly clumped in both 2007 ($Z = 4.43$, $df = 107$, $P < 0.0001$) and 2008 ($Z = 7.23$, $df = 106$, $P < 0.0001$), with similar indices of aggregation (2007: $I_A = 0.64$; 2008: $I_A = 0.60$). For occupied burrows, there was no significant difference between the nearest neighbour distances between years ($t = 1.02$, $df = 152$, $P = 0.331$; Table 1). In both years, occupied burrows were significantly clumped (2007: $I_A = 0.77$, $Z = 4.43$, $df = 79$, $P < 0.0001$; 2008: $I_A = 0.70$, $Z = 5.41$, $df = 72$, $P < 0.0001$). However, the spatial distribution of burrows differed between years (Fig. 1) with those containing adults being more clustered than those with juveniles, and areas where burrows were found in one year but not in the other.

For each year, the occupied burrow size was significantly positively correlated with spider body length (2007: $r = 0.376$, $n = 48$, $P = 0.008$; 2008: $r = 0.424$, $n = 26$, $P = 0.031$; Fig. 2), and in general larger spiders were found in larger burrows with some exceptions of small juveniles inhabiting what appeared to be abandoned adult burrows.

Despite similar numbers of burrows being found in both years, the locations were markedly different, suggesting that individuals move between pre-existing burrows or to new burrows. Examination of the clearing in 2008 revealed no visible signs of old burrows in areas where burrows had previously been present. This could be due to burrow structure as *B. vagans* can have up to four chambers off the main burrow (Machkour-M'Rabet et al. 2007) and be recorded at depths of 3–40cm (Machkour-M'Rabet et al. 2007) and up to 50 cm (Shaw pers. obs.). Rainfall can be high during the wet season, and the clearing is subject to seasonal flooding, which, coupled with the lack of deep roots, could lead to burrow collapse. Of those burrows matching between 2007 and 2008 some were protected from collapse, being underneath the edges of buildings, rocks and large roots. Burrow orientation can make them more susceptible to rain-carrying winds, helping to maintain high humidity (Machkour-M'Rabet et al. 2005), but leading to a trade-off between optimum humidity and having to move when flooded. Certainly areas that regularly flood have almost no burrows, and those at the edge of the flood zone can become waterlogged, resulting in tarantulas sitting huddled at the mouth of the burrow until the water subsides. Repeated flooding could result in abandonment, as observed in other burrowing spiders (Marshall 1995). Abandoned burrows would then be free for juveniles, possibly explaining the low correlation between spider stage and burrow size.

The nearest neighbour analysis showed similar mean distances between burrows in the North of Belize, as found by Reichling (1999: 3.4 m), and those at Las Cuevas (3.88 m, 2007; 3.16 m, 2008), suggesting that there may be an optimal distance driven by competitive repulsion (Reichling 1999). The level of between-year movement implied by this study may be due to relocation of juveniles prior to reaching maturity. Machkour-M'Rabet et al. (2005) found that adults and juveniles aggregated separately, although this is not evident in the study population. Reichling (1999) suggests that aggregative tendencies in theraphosids could reduce exposure to predators and increase reproductive success of nomadic males due to the shorter roaming distances required between feeund females. This can further be aided by the presence of detectable chemical cues (Yañez et al. 1999).

Dor et al. (2008) found females readily enter burrows of other females, sometimes resulting in the attack and death of one of them (Hénaut and Machkour-M'Rabet 2005). With high densities and clustered burrows, it is possible that there is frequent burrow takeover, particularly since chemical cues left by the silk at the burrow mouth can attract females to each other (Dor et al. 2008).

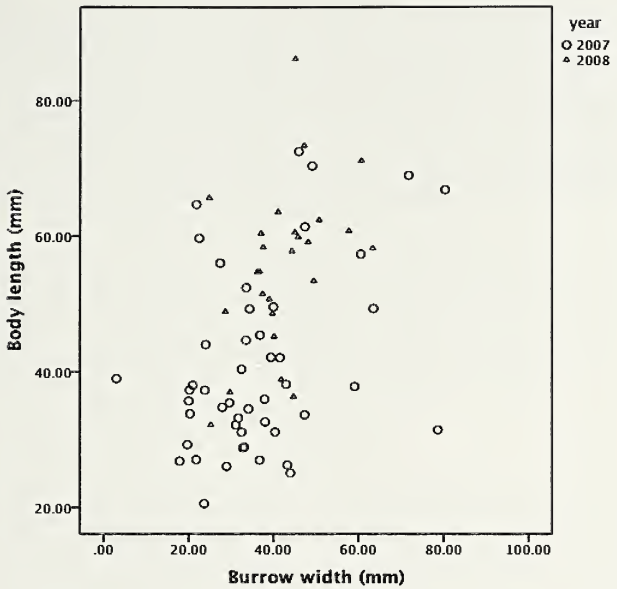


Figure 2.—Correlation between the body size of *B. vagans* tarantulas and the width of their burrows at Las Cuevas Research Station, Belize in 2007 and 2008.

In conclusion, this study highlights that the population of *B. vagans* at Las Cuevas Research Station is stable and highly mobile. In 2007 much of the captured population was composed of juveniles, whereas in 2008 more were adults, suggesting that the population is developing and indicating a potential population boom as the large number of adults produce juveniles. If this is the case, continued studies on this population should help elucidate some patterns of dispersal and distribution.

ACKNOWLEDGMENTS

The authors would like to thank all the students on the Manchester Metropolitan University and the University of Manchester Belize field course, Vicky Ogilvy, who assisted with collecting individuals, and Las Cuevas Research Station and the Belize Forestry Department for allowing this work to be conducted.

LITERATURE CITED

Coddington, J.A. & H.W. Levi. 1991. Systematics and evolution of spiders (Araneae). Annual Review of Ecology and Systematics 22:565–592.

Dor, A., S. Machkour-M'Rabet, L. Legal, T. Williams & Y. Hénaut. 2008. Chemically mediated burrow recognitition in the Mexican tarantula *Brachypelma vagans* female. Naturwissenschaften 95:1189–1193.

Edwards, G.B. & L.H. Hibbard. 1999. The Mexican redrump, *Brachypelma vagans* (Araneae: *Theraphosidae*), an exotic tarantula established in Florida. Entomology Circular 394. Department of Agriculture & Consumer Services, Division of Plant Industry, Gainesville, Florida.

Hénaut, Y. & S. Machkour-M'Rabet. 2005. Canibalismo y cleptobiosis en la tarántula *Brachypelma vagans*. Entomology Mexican 4:30–32.

Krebs, C.J. 1999. Ecological Methodology, 2nd Edition. Addison-Wesley Educational Publishers, New York.

Locht, A., M. Yañez & I. Vasquez. 1999. Distribution and natural history of Mexican species of *Brachypelma* and *Brachypelmides* (Theraphosidae, Theraphosinae) with morphological evidence for their synonymy. Journal of Arachnology 27:196–200.

Longhorn, S.J. 2002. Non-lethal DNA sampling from CITES II protected 'tarantula' spiders of Belize. Las Cuevas Newsletter 9:8–9.

Longhorn, S.J., M. Nicholas, J. Chuter & A.P. Volger. 2007. The utility of molecular markers from non-lethal DNA samples of the CITES II protected "tarantula" *Bracypelma vagans* (Araneae, Theraphosidae). Journal of Arachnology 35:278–292.

Machkour-M'Rabet, S., Y. Hénnaut, R. Roberto & S. Calmé. 2005. A not so natural history of the tarantula *Brachypelma vagans*: Interaction with human activity. Journal of Natural History 39:2515–2523.

Machkour-M'Rabet, S., Y. Hénnaut, A. Sepulveda, R. Rojo, S. Clamé & V. Geissen. 2007. Soil preference and burrow structure of an endangered tarantula, *Brachypelma vagans* (Mygalomorphae: Theraphosidae). Journal of Natural History 41:1025–1033.

Machkour-M'Rabet, S., Y. Hénnaut, A. Dor, G. Perez-Lachaud, C. Pelissier, C. Gers & L. Legal. 2009. ISSR (Inter Simple Sequence Repeats) as molecular markers to study genetic diversity in Tarantulas (Mygalomorphae). Journal of Arachnology 37:10–14.

Marshall, S.D. 1995. Mechanisms of the formation of territorial aggregations of the burrowing wolf spider *Geolycosa xera archboldi* McCrone (Araneae, Lycosidea). Journal of Arachnology 23:145–150.

Marshall, S.D. 1996. Evidence for territorial behaviour in a burrowing wolf spider. Ethology 102:32–39.

Perez-Miles, F., S.M. Lucas, P.I. da Silva, Jr. & R. Bertani. 1996. Systematic revision and cladistic analysis of Theraphosinae (Araneae: Theraphosidae). Mygalomorph 1:33–68.

Peterson, S.D., T. Mason, S. Akbar, R. West, B. White & P. Wilson. 2006. Species identification of tarantulas using exuviae for international wildlife law enforcement. Conservation Genetics 8:497–502.

Reichling, S.B. 1999. Spatial relationships of theraphosid spiders in Belize. Southwestern Naturalist 43:518–521.

Reichling, S.B. 2000. Group dispersal in juvenile *Brachypelma vagans* (Araneae, Theraphosidae). Journal of Arachnology 28:248–250.

Reichling, S.B. 2003. Tarantulas of Belize. Krieger Publishing Company, Malabar, Florida.

Smith, A. 1986. The Tarantula: Classification and Identification Guide. Fitzgerald Publishing, London.

Valerio, C. 1980. Aranas Terafosidas de Costa Rica (Araneae: Theraphosidae). 1. *Sericopelma* y *Brachypelma*. Brenesia 18:288.

Wheater, C.P., J.R. Bell & P.A. Cook. 2011. Practical Field Ecology: A Project Guide. Wiley-Blackwell, London.

Yañez, M., A. Locht & R. Marcías-Ordóñez. 1999. Courtship and mating behavior of *Brachypelma klaasi* (Araneae, Theraphosidae). Journal of Arachnology 27:165–170.

Yañez, M. & G. Floater. 2000. Spatial distribution and habitat preference of the endangered tarantula, *Brachypelma klaasi* (Araneae: Theraphosidae) in Mexico. Biodiversity and Conservation 9:795–810.

Manuscript received 11 June 2010, revised 22 September 2011.

2011. The Journal of Arachnology 39:519–522

SHORT COMMUNICATION

Function of the upper tangle in webs of young *Leucauge argyra* (Araneae: Tetragnathidae)

Emilia Triana-Cambronero[1], **Gilbert Barrantes**[1], **Erica Cuyckens**[2] and **Andrés Camacho**[1]: [1]Escuela de Biología, Universidad de Costa Rica, Ciudad Universitaria Rodrigo Facio, San José, Costa Rica. E-mail: emit773@gmail.com; [2]CONICET, Mendoza 2, Salta 4400, Argentina

Abstract. Ontogenetic changes in web structure occur in many spiders of different families, but the functional adaptation of differences in web structure is unknown for most species. We describe the ontogenetic changes in web structure of *Leucauge argyra* (Walckenaer 1842) and test the function of these differences in webs of spiderlings. Webs of early instar spiders have tangles above the orb web that vary from relatively dense to a single thread, from which some threads extend downward, connecting the tangle to the hub of the orb web. The number of threads of the tangle decreases as spiders grow, and in webs of late instars, the tangle is absent. Our experimental results indicate that the tangle and connecting threads increase the stability of the web, possibly reducing the probability of spiral threads sticking to each other with web movements.

Keywords: Web structure, ontogenetic changes, web tangle, orb web

Change in web structure through successive instars is a pattern found in many spiders of different families (at least 21 species of 10 different families: see Eberhard et al. 2008), and some of these ontogenetic changes are substantial (Eberhard 1985; Barrantes & Madrigal-Brenes 2008). However, with few exceptions, there has been no functional adaptation associated with these intraspecific differences in web structure between webs of young and adult spiders for most species. To our knowledge, the functional significance of ontogenetic changes in web architecture has been described only for *Clitaetra irenae* Kuntner 2006 (Kuntner et al. 2008a) and *Nephila clavipes* (Linneaus 1767) (Higgins 1992). Webs of *C. irenae* increase vertically in older spiders, as a possible adaptation to an arboricolous life style, as well as increase their hub eccentricity, possibly to optimize prey capture (Masters and Moffat 1983; Kuntner et al. 2008a, b). In *N. clavipes*, the density and proportional size of the tangle decrease as the spider grows as a consequence of reduction in predation risk (Higgins 1992).

Spiders of at least five families add tangles to their orb webs: Uloboridae, Mysmenidae, Nephilidae, Tetragnathidae, and Araneidae. There are several possible explanations for the function of tangles associated with orbicular webs. One is that the tangles serve as a mechanical barrier to protect the spider against flying predators (Comstock 1912; Robinson & Robinson 1973; Higgins 1992) or parasites (Robinson & Robinson 1973). Two other possible functions are that the tangles prevent escape of large prey (Hingston 1992) and act as support to strengthen the web (Lubin 1975). Only Higgins (1992) provides strong, though correlative, evidence that supports the anti-predator function of this structure, and Lubin (1975) provides correlative data that seems to support the web-strengthening hypothesis, but to our knowledge, none of these hypotheses has yet been tested experimentally.

The web of a *Leucauge argyra* (Walckenaer 1842) early instar has an upper tangle with threads connecting it to the hub and occasionally another tangle below the orb web, but these tangles are absent in webs of adult spiders. The upper tangle consists of a few threads that cover only a narrow section across the middle of the orb, contrary to the three-dimensional orb-like tangles or barriers in some nephilids that cover the entire dorsal and/or ventral side of the webs (Kuntner et al. 2008b). We specifically tested 1) whether the tangle above the orb web and the threads that connect this structure to the hub prevents the orb web striking the vegetation below it and 2) if the function of the tangle is to give stability to the orbicular section of the web, reducing web deformation and the probability of sticky spiral threads collapsing with air movement (these hypotheses may not be mutually exclusive).

We made field observations and experiments in a plantation of African oil palm (*Elais guineensis* L.) in Parrita, Puntarenas Province, Costa Rica (09°30′N, 84°10′W, elev. 10 m). To test the first hypothesis, we measured the distance of the hub of the orb web to the nearest substrate below in 21 webs of young spiders with upper tangles. This distance was later compared with the total hub displacement: distance after disconnecting the hub from the upper tangle plus its displacement distance after disconnecting it and blowing a constant perpendicular air current through the web (see below).

To test the second hypothesis, we constructed a three-sided cardboard shield (30 × 60 × 30 cm, 40 cm high) with black fabric (for better contrast with the web) attached to the central wall, and a ruler attached to the fabric. We placed this retreat around each web in the field to block uncontrolled natural breezes. We then applied an air current at a constant speed (0.03 m/s) using a 9V-battery fan (Max Flow Enterprise Co., Ltd.) placed 14 cm above the center of the orb web, simulating a perpendicular breeze to the plane of the web. For each of 25 manipulated webs, we measured three variables: 1) downward displacement of the hub of the unmodified web when blown with the fan; 2) displacement of the hub when threads connecting the hub to the tangle above were cut (the spider was present in the hub when threads were cut); 3) displacement of the hub when blown with the fan, after cutting the attachments to the tangle. We measured total body length of all 25 spiderlings to later test for a correlation of body length with web displacement.

We additionally measured the extensibility of two (occasionally one) 1 cm long segments of anchor threads in 20 webs with upper tangles of young spiders (different from the ones used for the other experiments) and of six webs of adult females. We attached each segment to pieces of double-sided sticky tape that had previously been attached to the jaws of a mechanical calliper as in Opell et al. (2008); a second piece of tape was placed on the threads to secure them. We then slowly separated the jaws of the calliper (ca 1 mm/s) to elongate threads until they broke. We measured extensibility as a proportion of the total extension relative to the initial thread length. When we measured two segments from the same web, their values were averaged. We collected and raised, in captivity, to adulthood two young spiders with tangled webs to confirm species identity and deposited these specimens in the Museo de Zoología, Universidad de Costa Rica.

Figure 1.—Web characteristics of young *Leucauge argyra*. A. Web of a small spiderling with relatively dense tangle and numerous threads connecting the tangle to the hub of the orb web below. Part of the lower tangle with some threads attached to the substrate below is shown. B. Web of an older instar spiderling with a reduced tangle and few threads connecting the tangle to the hub of the orb web below. C. Web with radii and spiral threads deformed by a weak breeze in the field. D. Section of a spiderling web showing some spiral threads collapsed (white arrows).

Webs of *L. argyra* show clear ontogenetic changes. Adult females spin typical orb webs in horizontal planes (0–20°) without additional silk structures. They build them in open spaces, using exposed twigs and leaves on the herbaceous layer to attach the anchor threads. In contrast, early instar spiderlings (first instar out of the egg sac, recognized by their whitish abdomens, to possibly fourth instars, based on size) spin tangle structures above the horizontal orb webs (Figs. 1A, B). The tangle varies from a relatively dense, narrow tangle, to a few threads just a few mm above the orb. Several threads connect the hub to the tangle above. The tangle above the orb seems to be denser in younger spiderlings (Fig. 1A). In some webs, there is also a tangle of sparse threads that connect the web frame with the substrate below (Fig. 1A). Webs of early instars are constructed within dense herbaceous vegetation, often occupying small spaces among grass leaves.

Our results indicate that these tangles above the orb webs of early instar spiders serve to support the entire orb web. The distance between the orb webs and the nearest substrate below was much larger (mean = 12.09 ± 11.73 cm, $n = 21$) than the total distance displaced by the webs after we disconnected them from the tangle (4.02 ± 1.58 cm; *t*-test comparing both distances: $t_{40} = 3.12$, $P < 0.005$). The total distance included both the distance of displacement of the hub when disconnected from the tangle and the distance of displacement when blown after disconnected. Webs of young spiders displaced between 1 cm to 3.5 cm (mean = 1.6 ± 0.94 cm, $n = 25$) downward after we disconnected the upper tangle from the orb web. This distance differed significantly from zero (no effect on threads in supporting the web; one sample t-test: $t_{24} = 8.59$, $P < 0.00001$), but displacement distance was not correlated with spider size ($r = 0.49$, $P = 0.82$).

When we blew perpendicular air current on the webs after we disconnected the upper tangle, all but two of these webs displaced further down (mean = 2.4 ± 0.9 cm, $n = 25$) than intact webs with the same air current (mean = 1.4 ± 0.8 cm, $n = 25$; paired *t* test: $t_{24} = 6.12$, $P < 0.00001$; Fig. 2). A possible explanation for the two webs in which displacement was less after disconnecting them from the upper tangle is that anchor lines of webs of young spiders can often be attached to grass blades that seem to be under some tension. Thus, when we disconnected the webs from the upper tangle, tension on the orbs may have increased and so reduced the downward displacement. Extensibility of anchor threads was similar between webs of young spiders and those of adult females (1.88 ± 1.46 vs. 1.40 ± 0.66; Mann-Whitney $U = 51.0$, $P = 0.60$, $n = 26$).

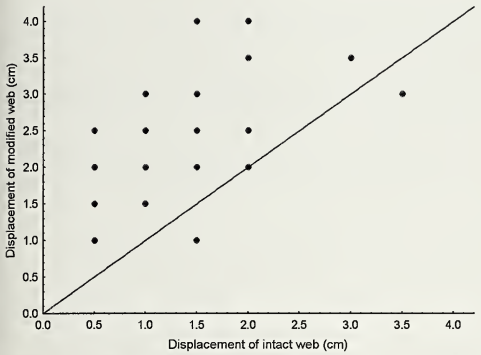


Figure 2.—Difference in displacement caused by a constant air current perpendicular to web plane, between intact webs (attached to the upper tangle) and the same webs after disconnecting them from the upper tangle. Dots above the line represent webs where displacement was larger after cutting the connecting threads. Line indicates equal effect of air current on intact and modified webs.

Despite young spiders constructing their webs among dense vegetation, the distance from the orb web to the nearest substrate below was large enough to prevent the orb web from contacting vegetation as it moved downward, even after the web was disconnected from the upper tangle. Therefore, our results do not support the hypothesis that the function of the upper tangle is to prevent the orb web from striking vegetation below.

Yet, webs of young *L. argyra* are slack. Under a nearly imperceptible breeze, the webs of young spiderlings buckle, the radii bending toward the wind's current trajectory and the spiral threads oscillating (Figs. 1C, D). Low tension of spiral threads makes webs good traps for retaining prey. Lower tension of these threads allows more kinetic energy to dissipate with the prey's impact (Eberhard 1990), but also make them susceptible to collapse in a weak breeze.

Damages of this type on the orb web are expected to reduce interception and retention of prey (Blackledge & Zevenbergen 2006). Hence, we conclude that the upper tangle serves as support for the whole orb web, allowing the spiderling to construct a well adapted trap to retain prey. The tangle likely reduces web deformation, which in turn may at least partially prevent sticky threads from adhering (Figs. 1C, D). A possible advantage of the stabilization of the web provided by the upper tangle is the reduction in radial stress and damage. This is important since strong winds could cause mechanical yield in radial threads, and thus will greatly reduce their ability to dissipate kinetic prey energy (Harmer et al. 2011).

We did not test the function of the lower tangle. This tangle consists of sparse threads that connect the frame of only some spiderling's webs to the substrate below (Fig. 1A). Thus, it is possible that this tangle gives additional support to the orb web and some protection against predators and parasitoids attacking spiders from below, a function that may also be possible for the upper tangle.

We also recorded ontogenetic changes in webs of *L. argyra* that occur mainly on the structure of the tangle. The complexity of the tangle and the number of threads that connect the tangle to the hub of the orb web below decrease as the spider grows. Tangles change from a relatively dense tangle with many connecting threads (up to 17) in very small spiderlings (Figs. 1A, B), to a sparse tangle composed of few threads in older instars (in two occasions the tangle was composed of a single thread with three connecting threads), to its complete absence in webs of adult females (not a single web of adult females had a tangle above it, $n > 300$ webs).

The extensibility of the anchor threads serves to absorb and dissipate some of the kinetic energy of a flying insect or the stress caused by wind currents (Denny 1976; Blackledge & Hayashi 2006). Webs of both early instar and adult *L. argyra* have similar extensibilities. Casual observations under a dissecting microscope suggest that the thickness of the anchor threads increases in the webs of older instar spiders. However, as the diameter of the anchor threads increases, more energy is needed to extend a thread the same distance. Therefore, such thicker threads in older instars provide more support against orb deformation, reducing the need for the upper tangle.

We here present the first experimental evidence of the possible function of the web design of first instar spiders. We also describe the ontogenetic changes in the web design of *L. argyra*. These changes are consistent with the general ontogenetic pattern documented for a large number of spider species in different families. Furthermore, in most species in which the ancestral-descendant evolution of webs can be traced, webs of first instar spiders nearly always represent ancestral characters (Japyassú & Ades 1998; Eberhard et al. 2008; Barrantes & Eberhard 2010). However, it is yet untested whether these ontogenetic changes mirror phylogenetic changes in web structure in this lineage (i.e., whether the silk tangle is an ancestral or derived character within the Orbiculariae).

ACKNOWLEDGMENTS

We thank William Eberhard, Linden Higgins, and two anonymous reviewers for their comments on previous versions of this manuscript. We also thank Diana Galindo for lending us the fan for the field experiments, the Organization for Tropical Studies for logistic support, and Don Pedro Gaspar for kindly allowing us to work in his plantation. This investigation was partially supported by the Vicerrectoría de Investigación, Universidad de Costa Rica.

LITERATURE CITED

Barrantes, G. & R. Madrigal-Brenes. 2008. Ontogenetic changes in the web and growth of *Tengella radiata* (Araneae, Tengellidae). Journal of Arachnology 36:545–551.

Barrantes, G. & W.G. Eberhard. 2010. Ontogeny repeats phylogeny in *Steatoda* and *Latrodectus* spiders. Journal of Arachnology 38:485–494.

Blackledge, T.A. & C.Y. Hayashi. 2006. Silken toolkits: biomechanics of silk fibers spun by the orb web spider *Argiope argentata* (Fabricius 1775). Journal of Experimental Biology 209:2452–2461.

Blackledge, T.A. & J.M. Zevenbergen. 2006. Mesh width influences prey retention in spider orb webs. Ethology 112:1194–1201.

Comstock, J.H. 1912. The Spider Book. Comstock Publishing Associates, Cornell University Press, New York.

Denny, M. 1976. The physical properties of spider's silk and their role in the design of orb-webs. Journal of Experimental Biology 65:483–506.

Eberhard, W.G. 1985. The "sawtoothed" orb web of *Eustala* sp. (Araneae, Araneidae) with discussion of ontogenetic changes in spiders' web-building behavior. Psyche 92:105–117.

Eberhard, W.G. 1990. Function and phylogeny of spider webs. Annual Review Ecology and Systematics 21:341–372.

Eberhard, W.G., G. Barrantes & R. Madrigal-Brenes. 2008. Vestiges of an orb-weaving ancestor? The "biogenic law" and ontogenetic changes in the webs and building behavior of the black widow spider *Latrodectus geometricus* (Araneae: Theridiidae). Ethology Ecology and Evolution 20:211–244.

Harmer, A.M.T., T.A. Blackledge, J.S. Madin & M.E. Herberstein. 2011. High-performance spider webs: integrating biomechanics, ecology and behaviour. Journal of the Royal Society Interface 8:457–471.

Higgins, L. 1992. Developmental changes in barrier web structure under different levels of predation risk in *Nephila clavipes* (Araneae: Tetragnathidae). Journal of Insect Behavior 5:635–655.

Hingston, R.W.G. 1992. The snare of the giant wood spider (*Nephila maculata*), part III: further lessons of the *Nephila*. Journal of the Bombay Natural History Society 28:917–923.

Japyassú, H.F. & C. Ades. 1998. From complete orb to semi-orb webs: developmental transitions in the web of *Nephilengys cruentata* (Araneae: Tetragnathidae). Behaviour 135:931–956.

Kuntner, M., C.R. Haddad, G. Aljančič & A. Blejec. 2008a. Ecology and web allometry of *Clitaetra irenae*, an arboricolous African orb-weaving spider (Araneae, Araneoidea, Nephilidae). Journal of Arachnology 36:583–594.

Kuntner, M., J.A. Coddington & G. Hormiga. 2008b. Phylogeny of extant nephilid orb-weaving spiders (Araneae, Nephilidae): testing morphological ethological homologies. Cladistics 24:147–217.

Lubin, Y.D. 1975. Stabilimenta and barrier webs in the orb webs of *Argiope argentata* (Araneae, Araneidae) on Daphne and Santa Cruz Islands, Galapagos. Journal of Arachnology 2:119–126.

Masters, W.M. & A.J.M. Moffat. 1983. A functional explanation of top-bottom asymmetry in vertical orbwebs. Animal Behaviour 31:1043–1046.

Opell, B.D., B.J. Markley, C.D. Hannum & M.L. Hendricks. 2008. The contribution of axial fiber extensibility to adhesion of viscous capture threads spun by orb-weaving spiders. Journal of Experimental Biology 211:2243–2251.

Robinson, M.H. & B. Robinson. 1973. Ecology and behavior of the giant wood spider *Nephila maculata* (Fabricius) in New Guinea. Smithsonian Contributions to Zoology 149:1–76.

Manuscript received 11 April 2011, revised 29 September 2011.

2011. The Journal of Arachnology 39:523–527

SHORT COMMUNICATION

The genus *Plesiophrictus* Pocock and revalidation of *Heterophrictus* Pocock (Araneae: Theraphosidae)

José Paulo Leite Guadanucci: Universidade Federal dos Vales do Jequitinhonha e Mucuri, Departamento de Ciências Biológicas, Laboratório de Zoologia de Invertebrados, Campus JK, Rodovia MGT 367 – Km 583, n° 5000, Alto da Jacuba, Diamantina-MG, Brasil, CEP 39100-000. E-mail: joseguadanucci@gmail.com

Abstract. The genus *Plesiophrictus* is diagnosed and redescribed based on type material and additional specimens. The type species *P. millardi* (Pocock 1899) is redescribed. The genus *Heterophrictus* is revalidated, with *H. milleti* as type species. *Heterophrictus* differs from *Plesiophrictus* by the absence of serrula on maxillae and by having a rastellum on the chelicerae and stiff, spike-shaped setae on the prolateral coxae I. The significance of characters used in the taxonomy of both genera is discussed.

Keywords: Spider, taxonomy, India, Ischnocolinae, Eumephorinae, serrula

The genus *Plesiophrictus* was described by Pocock 1899 to accommodate three species (*P. collinus* Pocock 1899, *P. millardi* Pocock 1899, *P. tenuipes* Pocock 1899) from India and Sri Lanka, with *P. millardi* as the type species. As promised a year before, Pocock (1900) gave more precise descriptions of *Plesiophrictus* species in his book "Fauna of the British India" and, additionally, described the monotypic genus *Heterophrictus*, *H. milleti* as type species. According to Pocock, *Plesiophrictus* could be distinguished from *Heterophrictus* by the shape of thoracic fovea, being straight in the former, procurved in the latter. Simon (1903) diagnosed *Heterophrictus* by the presence of long setae above the suture of the prolateral face of the first coxae, the shape of thoracic fovea and the posterior sternal sigilla remote from sternal margin. Gravely (1915) stated that Pocock's distinction, based on slight differences in shape of the fovea, was very unsatisfactory. Gravely also considered the setae observed by Simon in *Heterophrictus* to be related to size and to be variable even among adults. Throughout the years, several species were included within *Plesiophrictus* without any revisionary study. In 1985, Raven considered *Plesiophrictus* a senior synonym of *Heterophrictus* and *Ischnocollela* Strand 1907, since they share all characters of generic significance, which were not mentioned by the author. Hitherto, the genus *Plesiophrictus* was comprised of 16 species distributed mainly in India and single records for Micronesia and Sri-Lanka.

METHODS

Specimens from the following institutions (giving acronym, city, and curator) were examined: BMNH – British Museum of Natural History, London, England. J. Beccaloni; MNHN – Muséum National d'Histoire Naturelle, Paris, France. C. Rollard; ZMUC – Zoological Museum, University of Copenhagen, Copenhagen, Denmark. N. Scharff.

All measurements, in mm, were taken with an ocular micrometer. The length of leg segments was measured between joints in dorsal view. Length and width of carapace, eye tubercle, labium and sternum are maximum values obtained. Total body length includes chelicerae and opisthosoma but not the spinnerets.

Terminology for the number and disposition of spines follows that of Petrunkevitch (1925), with modifications proposed by Bertani (2001).

Specimens were examined and illustrated using a Leica MZAPO stereoscopic microscope, with camera lucida. The spermathecae were cleared with carnation oil and illustrated in dorsal view. Left palpal bulbs were illustrated in pro and retrolateral views. Setae of male tibia I were removed in order to illustrate the tibial apophysis better.

For Scanning Eletronic Microscope images, the maxilla were left in absolute ethanol overnight, critical point dried and cleaned with an air spray. The material was glued to stubs with polyvinyl resin. The stubs were coated and observed under Scanning Eletronic Microscope JEOL JSM-6335F.

TAXONOMY

Family Theraphosidae Thorell 1869
Genus *Plesiophrictus* Pocock 1899

Plesiophrictus Pocock 1899:749, type species *Plesiophrictus millardi* Pocock 1899, by original designation; 1900:181; Gravely 1915:273 (part); Raven 1985:154; Siliwal et al. 2007:2853; Platnick 2011.

Ischnocolella Strand 1907:14, type species *Ischnocolella senffti* Strand 1907 by monotypy, type considered lost (Raven 1985). Synonimized by Raven 1985:155.

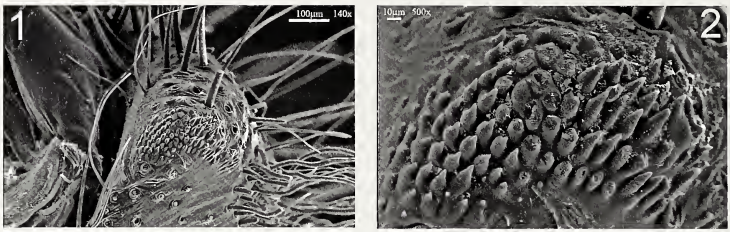
Diagnosis.—Representatives of the genus differ from those of *Heterophrictus* by the lack of stridulating apparatus or scopula on coxae or chelicerae and by the presence of serrula on the prolateral face of the maxillary lobe (Figs. 1, 2). Males can be recognized by the presence of short spines between the two tibial apophysis branches (Fig. 4).

Description.—Chelicerae without rastellum. Cephalic region weakly raised. Eye tubercle weakly raised, small. Anterior eye row procurved, posterior slightly recurved, clypeus absent. Thoracic fovea short, ranging from straight to slightly procurved. Labium as wide as long. Maxilla with produced anterior lobe, serrula present, cuspules on the inner angle. Posterior sternal sigilla remote from sternal margin. Cymbium with similar lobes. Tarsal scopula III–IV divided by a longitudinal band of thick setae. Superior tarsal claws without teeth, inferior tarsal claws absent, claw tufts well developed. Clavate tarsal trichobothria in two short rows, separated by a line of long and thin setae. Retrolateral scopula on femur IV absent. Stridulatory setae absent on coxae and chelicera. Urticating hairs absent. Posterior lateral spinnerets three-segmented, long, apical segment digitiform. Palpal bulb with tapering embolus, which bears a long basal keel. Male tibial apophysis present, formed by two branches, metatarsus I bends between the branches. Spermathecae formed by two receptacles, with single termini.

Plesiophrictus millardi Pocock 1899
Figs. 3–7

Plesiophrictus millardi Pocock 1899:749.

Plesiophrictus satarensis Gravely 1915; Siliwal et al. 2007:2859. New synonymy.



Figures 1, 2.—*Plesiophrictus collinus*. 1. Prolateral view of distal end of maxilla, showing the serrula; 2. Serrula denticles, detail.

Type material.—Holotype male of *P. nillardi* (BMNH) from Matheran, India; Holotype male of *P. satarensis* (BMNH 2205/17) from Medha, Yenna Valley, Satara District, Bombay, 17–23 April 1912; examined.

Other material examined.—*Plesiophrictus millardi*: 1 male, India, Uran (BMNH 99.11.2.234). *P. collinus*: holotype female, India, Yercaud (BMNH); 3 females and 1 juvenile, India, Madras, 21 December 1923 (BMNH); 1 female and 1 juvenile, India, Madras, R. Sherriffs leg., 20 November 1960 (ZMUC 635); 1 female, India, Vellore, Lowenthal leg., 24 April 1986 (ZMUC 624); 1 male, 2 females and 1 juvenile, India, Vellore, Lowenthal leg., 24 April 1986 (ZMUC 625). *P. sericeus*: holotype female, India, Poona (BMNH 99.11.2.116-117); 1 female, India, Poona (BMNH 99.9.21-161). *P. tenuipes*: holotype female, Sri Lanka, Kandy, Yevtriny leg. (BMNH 98.3.21.4).

Diagnosis.—It differs from the other species by the aspect of retrolateral branch of tibial apophysis (Figs. 3, 4), and by the helicoidal torsion of embolus on male palpal bulb (Figs. 5–7). Females unknown.

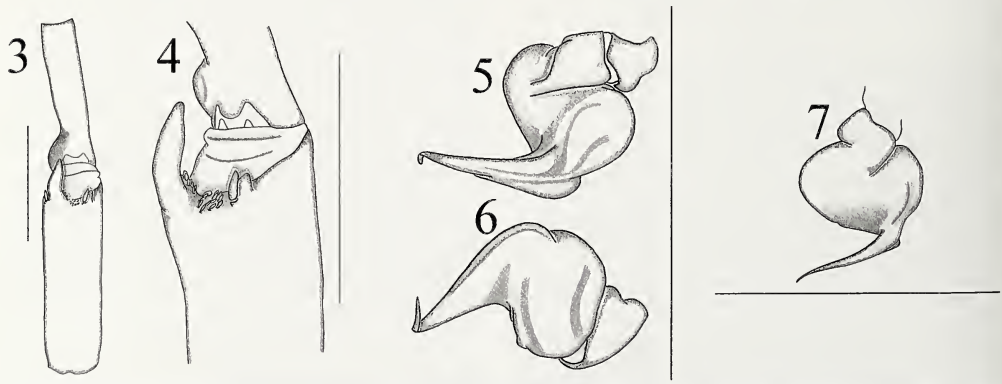
Description.—Male (holotype). Total length 14. Carapace: length 5.5; width 43. Eye tubercle: length 1.9; width 0.9. Labium: length 0.5; width 1. Sternum: length 2.5; width 2.4. Cheliceral basal segment with 9 teeth. Labium as wide as long with 14 cuspules. Maxilla with more than 45 cuspules, serrula present. Labiosternal suture with two distinct mounds. Sternum rounded, posterior sigilla remote from sternal margin. Thoracic fovea short and straight. Palp: femur 2.9/ patella 1.8/ tibia 2.2/ cymbium 1/ total 7.9. Legs I: femur 4/ patella 2.6/ tibia 2.9/ metatarsus 2.6/ tarsus 1.7/ total 13.8. II: 3.4/ 2.1/ 2.3/ 2.1/ 1.6/ 11.5. III: 3.1/ 1.8/ 1.8/ 2.2/ 1.6/ 10.5. IV: 4.2/ 2.2/ 3.2/ 3.4/ 1.9/ 14.9. Spines: Tarsi without spines. Palp without spines. Legs: I: metatarsus (v) ap1. II: tibia (v) ap2, (p) 0-0-1, metatarsus (v) ap1. III: patella (v) ap1, (p) 1, tibia (v) 1-1-ap3, (p) 2-2-0, (r) 1-1-0, metatarsus (v) 3-1-ap3, (p) 0-1-1, (r) 0-1-1. IV: femur (d) 0-0-r1, tibia (v) 2-2-ap3, (r) 0-1-1, metatarsus (v) 2-2-ap3, (p) 0-1-1, (r) 0-1-1. Male palpal bulb with tapering helicoidal embolus, bearing a basal long keel (Figs. 5–7). Tibial apophysis formed by two branches. Prolateral short with adjacent spine. Retrolateral bearing a spine inserted at midlength (Figs. 3, 4). Presence of several short spines between apophysis branches (Fig. 4). Metatarsus I straight, small retrolateral basal nodule, bends between two branches. Scopula on metatarsi: I–III apical half, IV less than apical half. Scopula on tarsi: I undivided, II undivided with a longitudinal band of setae, III–IV divided by a longitudinal band of thick setae. Superior tarsal claws without teeth, clavate trichobothria in two short rows divided by a line of long and thin setae. Eyes: anterior row procurved, posterior slightly recurved.

Genus *Heterophrictus* Pocock 1900

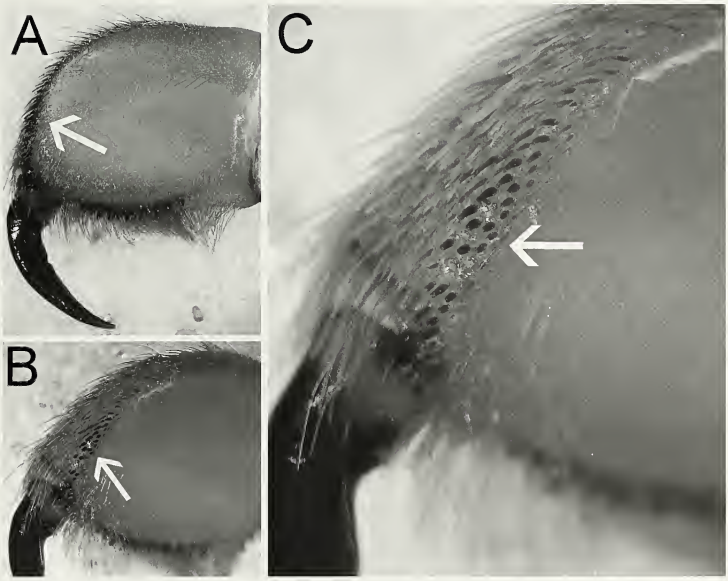
Heterophrictus Pocock 1900:180, type species *Heterophrictus milleti* Pocock 1900, by monotypy.

Plesiophrictus, Raven 1985:154 (synonymy, here rejected).

Diagnosis.—Representatives of the genus differ from those of *Plesiophrictus* by the presence of rastellum formed by a line of short spines on inner margin of dorsal surface of chelicerae (Fig. 8A–C) and stiff, spike-shaped setae above the suture on the prolateral coxae I (Fig. 9 A–C), and by the absence of serrula.

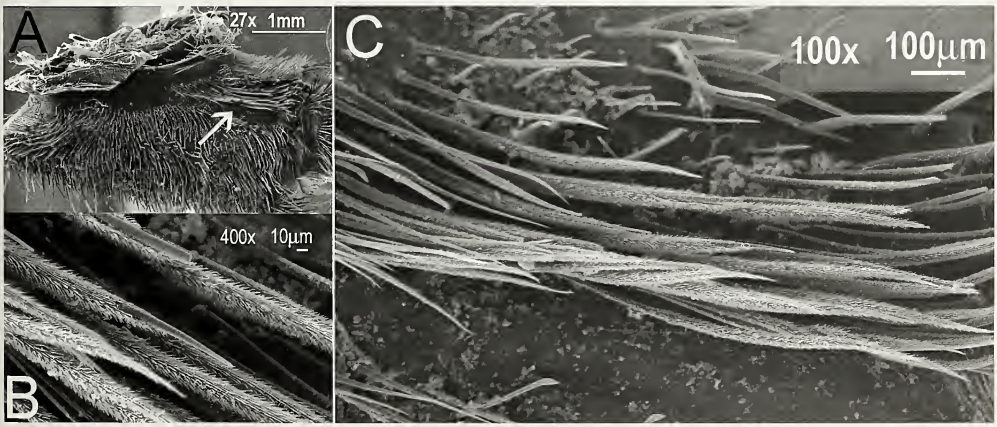


Figures 3–7.—*Plesiophrictus millardi*, Male holotype. 3. Tibial apophysis, ventral view; 4. Tibial apophysis, ventral-prolateral view; 5. Palpal bulb, prolateral view; 6. Palpal bulb, retrolateral view; 7. Palpal bulb, dorsal view. Scale = 1mm.



Figures 8.—A–C. *Heteroplirictus milleti*, right chelicerae: A. Prolateral view; B. Prolateral-frontal view; C. Detail of rastellum. Arrows showing rastellum.

Description.– Chelicerae with rastellum formed by a line of short spines on inner margin of dorsal surface of basal article. Cephalic region slightly raised. Eye tubercle weakly raised, small. Anterior eye row procurved, posterior slightly recurved, clypeus absent. Thoracic fovea straight or procurved. Labium as wide as long. Maxilla with produced anterior lobe, serrula absent, cuspules on the inner angle. Posterior sternal sigilla remote from sternal margin. Cymbium similar lobes. Tarsal scopula I–IV divided by a longitudinal band of thick setae. Superior tarsal claws without teeth, inferior tarsal claws absent, claw tufts well developed. Clavate tarsal trichobothria in two short rows, separated by a line of long and thin setae. Retrolateral scopula on femur IV absent. Stridulatory setae absent on chelicera. Stiff, thick, plumose setae above the suture on the prolateral surface of the coxae I (Figs. 8, 9). Urticating hairs absent. Posterior lateral



Figures 9.—A–C. *Heterophrictus milleti*: A. Maxilla, prolateral view, showing stiff setae; B. Detail of setae apex; C. Detail of stiff setae.

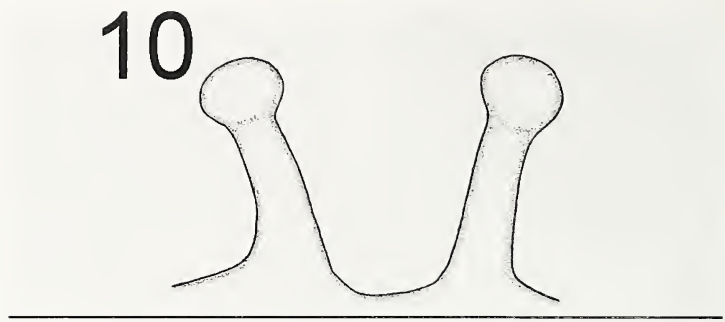


Figure 10.—*Heterophrictus milleti*, holotype female, spermathecae, dorsal view. Scale = 1mm.

spinnerets three-segmented, long, apical segment digitiform. Spermathecae formed by two receptacles, with single or multi termini.

Heterophrictus milleti Pocock 1900
Figs. 8–10

Heterophrictus milleti Pocock 1900:180.

Type material.—Holotype female (BMNH 99.9.21.162-3) from Násik, India; examined.

Other material examined.—*Ischnocolus linteatus*: holotype female, India, Pondichery (MNHN 5369); 1 female, India, Pondichery (MNHN 5372). *Plesiophrictus bhori*: paratype female, India, Parambikulan, 16–24 September 1914 (BMNH 16.5.2.16). *Plesiophrictus raja*: paratype female, India, Bombay, Helvak, Koyna Valley, Satara, 28–30 April 1912 (BMNH 16.5.2.15); paratype female, India, Kavalai, Kavali, 24–27 September 1914 (BMNH 16.5.2.17).

Diagnosis.—Females of *H. milleti* are distinguished by the spermathecae formed by two receptacula with a single terminus (Fig. 10) and by the thoracic fovea clearly procurved. Males unknown.

Description.—Female (holotype). Total length 20.6. Carapace: length 6.7; width 5.5. Eye tubercle: length 0.8; width 1.2. Labium: length 0.8; width 1.3. Sternum: length 3.1; width 3.1. Cheliceral basal segment with 13–14 teeth, rastellum formed by several short spines along the inner edge of dorsal cheliceral basal segment. Labium wider than long with 25 cuspules. Maxilla bearing nearly 80 cuspules, serrula absent. Labiosternal suture with two distinct mounds. Sternum rounded, posterior sigilla remote from sternal margin. Thoracic fovea procurved. Palp: femur 3.1/ patella 2.2/ tibia 2/ tarsus 1.8/ total 9.1. Legs I: femur 4.2/ patella 3.1/ tibia 3.1/ metatarsus 2/ tarsus 1.3/ total 13.7. II: 3.6/ 2.6/ 2/ 1.9/ 1.3/ 11.4. III: 3.1/ 2.2/ 1.8/ 2.5/ 1.6/ 11.2. IV: 4.6/ 2.7(tibia, metatarsus and tarsus IV missing). Spines: Tarsi without spines. Palp: tibia (v) ap1. Legs: I: metatarsus (v) ap1. II: tibia (v) ap1, metatarsus (v) ap1. III: patella (p) 1, tibia (v) 0-1-ap2, (r) 0-1-0, (p) 0-1-0, metatarsus (v) 0-2-ap3, (p) 0-1-1, (r) 0-1-1. Spermathecae formed by two long receptacula with distinct apical lobe (Fig. 10). Scopula on metatarsi: I–II apical half, III apical 1/3. Scopula on tarsi: all scopula divided. Superior tarsal claws without teeth, clavate trichobothria in two short rows. Eyes: anterior row procurved, posterior slightly recurved, clypeus absent.

DISCUSSION

Pocock (1900) used the shape of thoracic fovea to distinguish between *Plesiophrictus* and *Heterophrictus*. Although it is possible to distinguish the type species of the two genera, the examination of additional specimens of *Plesiophrictus* and *Heterophrictus* showed that this character is variable, in agreement with Gravely (1915).

Simon (1903) used the shape of thoracic fovea to diagnose both genera, but he also noted the presence of long setae on the prolateral surface of coxae I in *Heterophrictus milleti*. Scanning electron microscopy of coxae I revealed the ultrastructure of these setae. The stiff plumose setae are located above the suture of the coxae, which can be recognized under the stereomicroscope. These setae, in addition to the rastellum on the chelicera, also observed in *Heterophrictus milleti*, led me to propose the revalidation. Raven (1985) diagnosed the subfamily Eumenophorinae by the presence of long spike-shaped setae located on the prolateral coxae I at the dorsal portion. Such setae show the same morphology as those found in *Heterophrictus* (Fig. 9). Therefore, the genus *Heterophrictus* is transferred to the subfamily Eumenophorinae.

Concerning *Plesiophrictus*, the presence of maxillary serrula, which has never been reported for this genus, is an important character to diagnose the genus, along with the short spines between tibial apophysis of males.

Siliwal et al. (2007) diagnosed the genus *Plesiophrictus* based on the aspect of fovea, sternum sigilla, size of eyes and quantity of spines on legs, those of which do not warrant the recognition of the genus. The authors did not mention the characters to distinguish the two genera (presence of serrula, presence of chelicerae rastelum and coxae I with stiff setae).

Both genera discussed here are very difficult to study, because most of their species are only known from type material, which is scattered among museums in different countries. Moreover, of 16 species currently included within these genera, 10 are only known from the female.

The main purpose of this paper is to revalidate *Heterophrictus* and provide a diagnosis for *Plesiophrictus* and *Heterophrictus*. It is also important to highlight the need for a comprehensive revision of Indian theraphosids. The revision of these two genera must include all type material and the generic characters considered in the present study.

ACKNOWLEDGMENTS

I would like to thank the curators J. Beccaloni, C. Rollard and N. Scharff for having kindly hosted me during my visit to their institutions. Special thanks to Boris Striffler and Volker von Wirth for having shared information and descriptions on oriental Theraphosidae, for comments and suggestions on this manuscript. This study was carried out with financial support of CNPq (process 201036/2004-5) and it is part of the Ph.D. thesis of the author (CNPq process 142035/2003-3).

LITERATURE CITED

Bertani, R. 2001. Revision, cladistic analysis, and zoogeography of *Vitalius*, *Nhandu*, and *Proshapalopus*; with notes on other

theraphosinae genera (Araneae, Theraphosidae). Arquivos de Zoologia, São Paulo 36:265–356.

Gravely, F.H. 1915. Notes on Indian mygalomorph Spiders. Records of the Indian Museum Calcutta 11:257–287.

Petrunkevitch, A. 1925. Arachnida from Panamá. Boletín de la Sociedad Zoologica Uruguay (2° epoca) 7:11–12.

Platnick, N.I. 2011. The World Spider Catalog, Version 11.5. American Museum of Natural History, New York. Online at http://research.amnh.org/iz/spiders/catalog. (Accessed 10 February 2011).

Pocock, R.I. 1899. Diagnoses of some new Indian Arachnida. Journal of the Bombay Natural History Society 12:744–753.

Pocock, R.I. 1900. The Fauna of British India, Including Ceylon and Burma. Volume 7. Arachnida. Taylor and Francis, London.

Raven, R.J. 1985. The spider infraorder Mygalomorphae (Araneae): cladistics and systematics. Bulletin of the American Museum of Natural History 182:1–180.

Siliwal, M., S. Molur & R. Raven. 2007. A new species of the genus *Plesiophrictus* (Araneae: Theraphosidae: Ischnocolinae) from Western Ghats, India. Zoos' Print Journal 22:2853–2860.

Simon, E. 1903. Histoire naturelle des araignées. Librairie encyclopédique de Roret, Paris 2:669–1080.

Strand, E. 1907. Avicullariidae und Atypidae des Kgl. Naturalienkabinetts in Stuttgart. Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg 63:1–100.

Manuscript received 30 August 2010, revised 6 March 2011.

2011. The Journal of Arachnology 39:528–532

SHORT COMMUNICATION

On the *Avicularia* (Araneae: Theraphosidae: Aviculariinae) species from Uruguay

Caroline Sayuri Fukushima[1,3], **Fernando Pérez-Miles**[2] and **Rogério Bertani**[3]: [1]Pós-graduação do Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, Rua do Matão, Travessa 14, 321, CEP 05422—970, São Paulo – SP, Brazil; E-mail: carolsayuri@usp.br; [2]Sección Entomología, Facultad de Ciencias, Iguá 4225, 11400 Montevideo, Uruguay; [3]Instituto Butantan, Avenida Vital Brazil, 1500, CEP 05503—900, São Paulo – SP, Brazil

Abstract. The taxonomic status of four species of *Avicularia* Lamarck 1818 described from Uruguay: *Avicularia anthracina* (C.L. Koch 1842), *Avicularia alticeps* (Keyserling 1878), *Avicularia parva* (Keyserling 1878) and *Avicularia tigrina* (Pocock 1903) is discussed. The holotypes and/or original descriptions of these species were examined, and two taxonomic synonymies are needed, which are presented herein. *Avicularia anthracina* is transferred to *Grammostola*, resulting in *Grammostola anthracina* (C.L. Koch 1842) new combination and is considered a senior synonym of *Grammostola mollicoma* Ausserer 1875 new synonymy. Likewise, *Avicularia parva* is transferred to *Catumiri* Guadanucci 2004, where it is placed in the synonymy of *Catumiri uruguayense* Guadanucci 2004 new synonymy. *Avicularia tigrina* and *Avicularia alticeps*, originally described in the genera *Ischnocolus* Ausserer 1875 and *Pterinopelma* Pocock 1901, respectively, are herein considered nomina dubia since their types are presumed lost.

Keywords: Taxonomy, *Eurypelma*, *Mygale*, *Isclmocolus*, *Pterinopelma*

To date, the known Uruguayan theraphosid fauna comprises 18 species of the genera *Acanthoscurria* Ausserer 1871, *Eupalaestrus* Pocock 1901, *Grammostola* Simon 1892, *Catumiri* Guadanucci 2004, *Homoeomma* Ausserer 1871, *Lasiodora* C.L. Koch 1850, *Plesiopelma* Pocock 1901 and *Avicularia* Lamarck 1818 (Platnick 2010). Uruguay is a well-sampled country (Pérez-Miles et al. 1993), with many taxonomic studies on the family (Schiapelli & Gerschman de Pikelin 1964, 1970; Gerschman de Pikelin & Schiapelli 1972; Pérez-Miles 1992; Guadanucci 2004), being one of the best known theraphosid faunas in the world, even though some questions remain to be resolved. One of these questions is the presumed presence of *Avicularia* species in Uruguay, inconsistent with the known geographic distribution of the genus, which is otherwise limited to Southeastern Brazil (Bertani & Fukushima 2009). Four *Avicularia* species are described from Uruguay (Platnick 2010): *Avicularia anthracina* (C.L. Koch 1842), *Avicnlaria alticeps* (Keyserling 1878), *Avicularia parva* (Keyserling 1878), and *Avicularia tigrina* (Pocock 1903) (Platnick 2010).

Avicularia anthracina was described by C.L. Koch (1842) as *Mygale anthracina* but was later transferred to *Eurypelma* C.L Koch 1850 by C.L.Koch (1850). After this transfer, the species name has rarely been cited except in arachnological catalogs (Roewer 1942, 1955). *Avicularia tigrina* was originally described as *Pterinopelma tigrina* Pocock 1903. Simon (1903) considered the genus *Pterinopelma* Pocock 1903 a junior synonym of *Eurypelma* C.L. Koch 1842. *Avicularia parva* and *Avicularia alticeps* were described by Keyserling (1878) in *Ischnocolns* Ausserer 1875. According to Simon (1903), the American species of *Isclmocolus* described by Ausserer and Keyserling were, in general, immature *Eurypelma* C.L. Koch 1850 or *Lasiodora* C.L. Koch 1850. The author clearly affirmed that *Isclmocolus parvus* Keyserling 1878 is an immature specimen of *Eurypelma*, but he did not do the same for *Ischnocolus alticeps* Keyserling 1878. However, both were cited as a species of *Eurypelma* by later authors (Roewer 1942). All the four species were included in *Eurypelma* until Raven (1985) proposed the synonymy of *Eurypelma* with *Avicularia* Lamarck 1818, establishing several new implicit combinations, among them *Avicularia anthracina* (C.L. Koch 1842), *Avicularia parva* (Keyserling 1878), *Avicularia alticeps* (Keyserling 1878) and *Avicularia tigrina* (Pocock 1903). These four Uruguayan species are revised and their taxonomic position reinterpreted as part of a taxonomical revision of the speciose genus *Avicularia*, which is being carried out by the authors.

METHODS

All measurements are in millimeters and were obtained with a Mitutoyo calliper. We took leg and palp measurements from the dorsal aspect of the left side (unless appendages were lost or obviously regenerated). A Nikon SMZ1500 and a Leica MZ 125 dissecting microscope were used for illustrations (with a camera lucida attachment). Abbreviations: ALE = anterior lateral eyes, AME = anterior median eyes, ITC = inferior tarsal claw, PLE = posterior lateral eyes, PME = posterior median eyes, PMS = posterior median spinnerets, STC = superior tarsal claws. Specimens from the following institutions were examined: BMNH— British Museum of Natural History, London; ZMB —Museum für Naturkunde, Berlin. Urticating hair terminology follows Cooke et al. (1972).

TAXONOMY

***Catumiri parvum* (Keyserling 1878)** new combination
(Fig. 1)

Ischnocolus parvus Keyserling 1878:611; Bonnet 1957:2305.
Eurypelma parvum Roewer 1942:241.
Catumiri uruguayense Guadanucci 2004:7, figs.10–15 new synonymy
Oligoxystre argentinense Costa et al. 2000:131 (misidentification); Costa & Pérez-Miles 2002:571 (misidentification).
Avicularia parva Platnick 2010.

Material examined.—Holotype, immature male of *Ischnocolus parvus* from Uruguay, BMNH 1890-7.1.341. Holotype male (IBSP 9491) and paratype female (IBSP 9507) of *Catumiri uruguayense* from Lavalleja, Águas Blancas; Uruguay, F.Pérez-Miles leg., 22 November 1993.

The *Ischnocolus parvus* holotype is a small immature theraphosid specimen (carapace length 3.2 mm). Even though it has no fully developed genitalia, it exhibits some unusual theraphosid somatic characters such as the absence of any type of urticating hair, labium much wider than long (Fig. 1), few cuspules on maxilla (< 20), and absence of labial cuspules (Fig. 1). In the New World theraphosids,

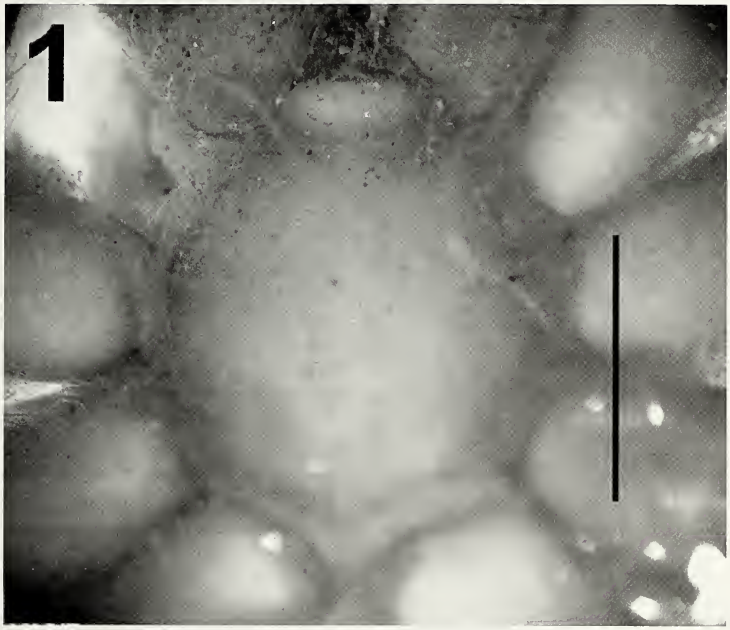


Figure 1.—*Catumiri parvum* (Keyserling 1878), holotype. Labium. Scale = 1mm.

absence of urticating hairs is characteristic of ischnocoline or some Amazonian avicularine taxa. Since this specimen has well-developed spines on the legs, absent in Avicularinae, the second option is discarded. The labium shape, absence of labial cuspules, and small number of cuspules on the maxillae are shared in South America by only two ischnocoline genera, *Oligoxystre* and *Catumiri*. *Oligoxystre* is not known from Uruguay or southern Brazil, so the unique ischnocoline genus so far known in Uruguay is *Catumiri* Guadanucci 2004, with a single species in the country, *C. uruguayense* Guadanucci 2004. Furthermore, the holotype of *Catumiri uruguayense* Guadanucci 2004 is morphologically consistent with the holotype of *Ischnocolus parvus* Keyserling 1878. So, we have decided to transfer *A. parva* to *Catumiri* and consider *Catmiri parvum* (Keyserling 1878) a senior synonym of *Catumiri uruguayense* Guadanucci 2004 **new synonymy**.

***Grammostola anthracina* (C.L. Koch 1842)** new combination
(Figs. 2–4)

Mygale anthracina C.L. Koch 1842:77, fig. 739; Simon 1892:172; Bonnet 1955:2992.

Eurypelma anthracina C.L. Koch 1850:73.

Eurypelma anthracinum Roewer 1942:238, 1954:1594.

Eurypelma molliconum Ausserer 1875:198; Keyserling 1878:612, pl. 14, fig. 28

Citharoscelus mollicomus Pocock 1903:99.

Grammostola mollicoma Simon 1903:935; Strand 1907:35; Petrunkevitch 1911:68; Mello-Leitão 1923: 211; Bücherl, 1951:109, 172–183, 190, figs. 3.II, 28.II, 29, pls. I, II; Roewer, 1954:1508; Bücherl 1957:395, fig. 55; Schiapelli & Gerschman 1961:202, figs. 13, 14; Pérez-Miles 1989:264, figs. 1, 2, 6–8; Costa & Pérez-Miles 2002:571; Pérez-Miles 2006:9–11; Postiglioni & Costa 2006:71; Costa & Pérez-Miles 2007:40; Panzera et al. 2009:92 new synonymy.

Phrixotrichus molicommus Pérez-Miles et al. 1996:54, figs. 36, 37.

Avicularia anthracina Platnick 2010.

Material examined.—Holotype female of *Eurypelma anthracinum* C.L. Koch 1842 from Montevideo, Uruguay, Sello leg., ZMB-2040. *Eurypelma mollicomum* Ausserer 1875 holotype female from Uruguay, Keyserling collection BMNH 90.7.1.388.

Redescription.—*Female holotype*: Total length, not including chelicerae or spinnerets 44.0 (Fig. 2). Cephalothorax 19.9 long, 21.0 wide. Legs (femur, patella, tibia, metatarsus, tarsus, total): I: 16.10, 10.20, 11.90, 10.25, 6.80, 55.25; II: 14.86, 8.52, 12.17, 10.36, 6.77, 52.68; III: 13.85, 7.60, 9.31, 10.98, 6.52, 48.26; IV: 15.98, 8.41, 12.78, 15.17, 7.90, 60.24; palp: 11.31, 6.96, 7.56, –, 6.86, 32.69. Anterior eyes row procurved, posterior row recurved. Eyes sizes and inter-distances: AME 0.45, ALE 0.60, PME 0.33, PLE 0.60, AME–AME 0.49, AME–ALE 0.31, AME–PME 0.09, ALE–ALE 1.87, ALE–PME 0.50, PME–PME 1.37, PME–PLE 0.13, PLE–PLE 2.10, ALE–PLE 0.38. Eye tubercle: length 2.5, width 2.75; clypeus absent. Fovea: deep, procurved, 3.0 long. Cephalic area raised. Thoracic striae conspicuous. Labium: length 3.3, width 3.9, with approximately 110 cuspules. Maxillae: between 100–200 cuspules spread over internal face. Tarsi I–IV fully scopulate. Metatarsi I–III scopulate on apical half, metatarsi IV scopulate on apical ¼. Urticating hair types III and IV present. Stridulatory setae on prolateral coxae I (Fig. 3). Color pattern: Cephalothorax and abdomen dark brown. Two long spermathecae with rounded apex (Fig. 4). Sternum and spinnerets damaged. Spines on all legs, but specimen too fragile for counting spination and disposition of spines in each leg and articles.

Figure 2.—*Grammostola anthracina* (C.L. Koch 1842) holotype female. General aspect. Scale = 10 mm.

Remarks.—The holotype has all characteristics of the genus *Grammostola*: two long spermathecae with rounded apex (Fig. 4), stridulatory setae on the prolateral coxae I (Fig. 3) and presence of urticating hairs type III and IV on dorsal abdomen. Consequently we have transfered the species to *Grammostola* Simon 1892. The dimensions and characteristics of the holotype of *Grammostola anthracina* match the holotype of *Grammostola mollicoma* Ausserer 1875 (examined). Thus, we decided to propose *Grammostola anthracina* (C. L. Koch 1842) as a senior synonym of *Grammostola mollicoma* (Ausserer 1875) **new synonymy**.

***Ischnocolus alticeps* Keyserling 1878** nomen dubium

Ischnocolus alticeps Keyserling 1878:609; Bonnet 1957:2302.
Eurypelma alticeps Roewer 1942:238; 1955:1533.
Avicularia alticeps Platnick 2010.

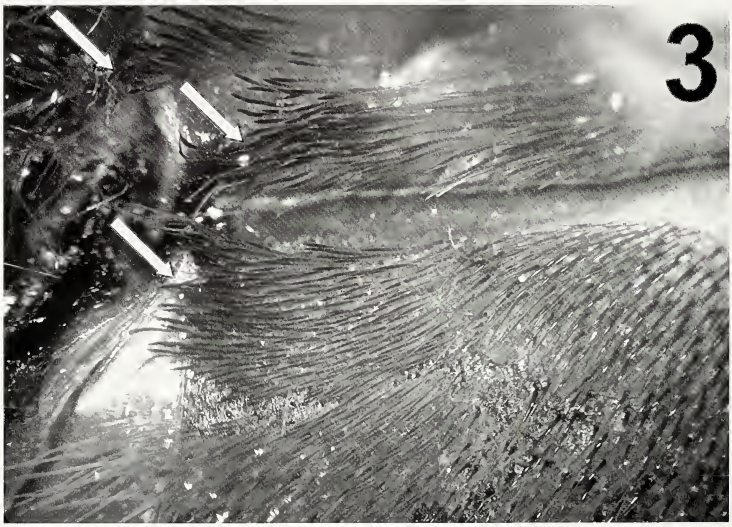


Figure 3.—*Grammostola anthracina* (C.L. Koch 1842) holotype female. Stridulatory setae (arrows) on prolateral coxae I.

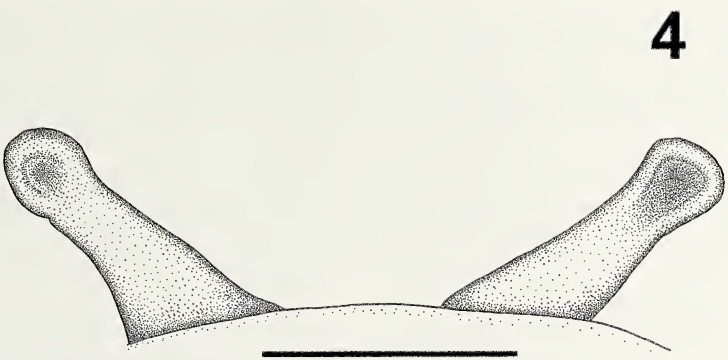


Figure 4.—*Grammostola anthracina* (C.L. Koch 1842) holotype female. Spermathecae, ventral. Scale = 1 mm.

Comments.—Holotype is herein considered lost. The holotype of *Avicularia alticeps* originally described in the genus *Ischnocolus* Ausserer 1875 was not found in the BMNH, where Keyserling's collection is housed. The authors have been in BMNH in different years and have never found the type. The curator also confirmed that the type is not there. Searches in other collections have also failed.

The description made by Keyserling does not contain any information that could allow us to identify the species. The author describes a female, but there is no characterization of its spermathecae. However, it is clear that it is not an avicularíine, since it has several spines on legs. As the species' identity is not clear, we consider the name *Ischnocolus alticeps* a nomen dubium.

***Pterinopelma tigrinum* Pocock 1903** nomen dubium

Pterinopelma tigrinum Pocock 1903:109; Bonnet 1955:1830, 1957:3828.
Eurypelma tigrinum Simon 1903:937; Roewer 1942:242.
Avicularia tigrina Platnick 2010.

Comments.—Holotype is herein considered lost. The holotype of *Avicularia tigrina* originally described in the genus *Pterinopelma* Pocock 1901 was not found in the BMNH, where Pocock's collections are housed. Both the authors and the BMNH curator have searched for the type without success.

The description mentions that the type presents spines on its legs, which indicates it is not an avicularíine. The author mentions presence of plumose bristles on some appendages and color details, "upperside of patellae and tibiae with conspicuous pale yellow bands." The described characteristics are present in more than one Uruguayan theraphosine species, making it impossible to know the species described by the author. As the identity of species is not clear, we consider the name *Pterinopelma trigrinum* a nomen dubium.

ACKNOWLEDGMENTS

We would like to thank Mr. Paul Hillyard and Mrs. Janet Becalloni from BMNH, Dr. Jason Dunlop and Mrs. Anja Friedrichs from ZMB for their help and kindness in loaning specimens and allowing the access of the authors to the arachnid collections. RB thanks Volker von Wirth and Andrew Smith for their hospitality when in Europe consulting arachnological collections. Support: FAPESP 03/12587-4 and CNPq Research Fellow for RB and FAPESP 06/58326-5 for CSF.

LITERATURE CITED

Ausserer, A. 1875. Zweiter Beitrag zur Kenntniss der Arachniden-Familie der Territelariae Thorell (Mygalidae Autor). Verhandllungen der kaiserlich-kongiglichen zoologish-botanischen Gesellschaft in Wien 25:125–206.

Bertani, R. & C.S. Fukushima. 2009. Description of two new species of *Avicularia* Lamarck 1818 and redescription of *Avicularia diversipes* (C.L. Koch 1842) (Araneae, Theraphosidae, Aviculariinae)—three possibly threatened Brazilian species. Zootaxa 2223:25–47.

Bonnet, P. 1955. Bibliographia araneorum. Toulouse 2(1):1–918.

Bonnet, P. 1957. Bibliographia araneorum. Toulouse 2(3):1927–3026.

Bücherl, W. 1951. Estudos sobre a biologia e a sistemática do gênero *Grammostola* Simon, 1892. Monografias do Instituto Butantan 1:1–203.

Bücherl, W. 1957. Sôbre a importância dos bulbos copuladores e das apófises tibiais dos machos na sistemática das aranhas caranguejeiras (Orthognatha). Anais da Academia brasileira de Ciências 29:377–416.

Cooke, J.A.L., V.D. Roth & F.H. Miller. 1972. The urticating hairs of theraphosid spiders. American Museum Novitates 2498:1–43.

Costa, F.G. & F. Pérez-Miles. 2002. Reproductive biology of Uruguayan theraphosids (Araneae, Mygalomorphae). Journal of Arachnology 30:571–587.

Costa, F.G. & F. Pérez-Miles. 2007. Cruel and irresponsible traffic of spiders in Uruguay. Arachne 12(3):40.

Costa, F.G., F. Pérez-Miles & S. Corte. 2000. Which spermatheca is inseminated by each palp in Theraphosidae spiders? : A study of *Oligoxystre argentinensis* (Ischnocolinae). Journal of Arachnology 28:131–132.

Gerschman de Pikelin, B.S. & R.D. Schiapelli. 1972. El género *Homoeomma* Ausserer 1871 (Araneae: Theraphosidae). Physis Buenos Aires (C) 31:237–258.

Guadanucci, J.P.L. 2004. Description of *Catumiri* n. gen. and three new species (Theraphosidae: Ischnocolinae). Zootaxa 671:1–14.

Keyserling, E. 1878. Spinnen aus Uruguay und einigen anderen Gegenden Amerikas. Verhandllungen der kaiserlich-kongiglichen zoologish-botanischen Gesellschaft in Wien 27:571–624.

Koch, C.L. 1842. Die Arachniden. Neunter Band, Nürnberg. Pp. 57–108.

Koch, C.L. 1850. Übersicht des Arachnidensystems. Heft 5, Nürnberg. Pp. 1–77.

Mello-Leitão, C.M. 1921. On the genus *Grammostola* Simon. Annals and Magazine of Natural History (9)7:293–305.

Mello-Leitão, C.M. 1923. Theraphosoideas do Brasil. Revista do Museu Paulista 13:1–438.

Panzera, A., C. Perdomo & F. Pérez-Miles. 2009. Spiderling emergence in the tarantula *Grammostola mollicoma* (Ausserer 1875): an experimental approach (Araneae, Theraphosidae). Journal of Arachnology 37:92–96.

Pérez-Miles, F. 1992. Revisión del género *Eupalaestrus* Pocock 1901 (Araneae, Theraphosidae). Revista Brasileira de Biologia 52:27–35.

Pérez-Miles, F., F.G. Costa & E. Gudynas. 1993. Ecologia de una comunidad de mygalomorphae criptozoicas de Sierra de Las Animas, Uruguay (Arachnida, Araneae). Aracnologia 17/18:1–22.

Pérez-Miles, F. 1989. Variacion relativa de caracteres somaticos y genitales en *Grammostola mollicoma* (Araneae, Theraphosidae). Journal of Arachnology 17:263–274.

Pérez-Miles, F. 2006. Die Biologie der Vogelspinnen Uruguays (Araneae, Theraphosidae). Arachne 11(3):4–15.

Pérez-Miles, F., S.M. Lucas, P.I. da Silva, Jr. & R. Bertani. 1996. Systematic revision and cladistic analysis of Theraphosinae (Araneae: Theraphosidae). Mygalomorph 1:33–68.

Petrunkevitch, A. 1911. A synonymic index-catalogue of spiders of North, Central and South America with all adjacent islands, Greenland, Bermuda, West Indies, Terra del Fuego, Galapagos, etc. Bulletin of the American Museum of Natural History 29:1–791.

Postiglioni, R. & F. Costa. 2006. Reproductive isolation among three populations of the genus *Grammostola* from Uruguay (Araneae, Theraphosidae). Iheringia 96:71–74.

Platnick, N.I. 2010. The World Spider Catalog, Version 10.5. American Museum of Natural History, New York. Online at http://research.amnh.org/entomology/spiders/catalog/INTRO1.html. Accessed 7 January 2010.

Pocock, R.I. 1903. On some genera and species of South American Avicularíidae. Annals and Magazine of Natural History (7)11: 81–115.

Raven, R.J. 1985. The spider infraorder Mygalomorphae (Araneae): cladistic and systematics. Bulletin of the American Museum of Natural History 182:1–180.

Roewer, C.F. 1942. Katalog der Araneae von 1758 bis 1940. Paul Budy, Bremen 1:1–1040.

Roewer, C.F. 1955. Katalog der Araneae von 1758 bis 1940, bzw. 1954. Institut royal des Sciences naturelles de Belgium, Bruxelles 2:1–1751.

Schiapelli, R.D. & B.S. Gerschman. 1961. Las especies del género *Grammostola* Simon 1892, en la República Argentina (Araneae, Theraphosidae). Actas y Trabajos del Congresso Sudamericano de Zoologia I (La Plata, 1959) 3:199–208.

Schiapelli, R.D. & B.S. Gerschman de Pikelin. 1964. El género *Acanthoscurria* Ausserer, 1871 (Araneae, Theraphosidae) en la Argentina. Physis Buenos Aires (C) 24:391–417.

Schiapelli, R.D. & B.S. Gerschman de Pikelin. 1970. El género *Ceropelma* Mello-Leitão, 1923 (Araneae, Theraphosidae). Physis Buenos Aires (C) 30:225–239.

Simon, E. 1892. Histoire naturelle des araignées. Libraire Encyclopédique de Roret, Paris 1:1–256.

Simon, E. 1903. Histoire naturelle des araignées. Libraire Encyclopédique de Roret, Paris 2:669–1080.

Strand, E. 1907. Avicularíidae und Atypidae des Kgl. Naturalienkabinetts in Stuttgart. Jahreshefte des Vereins fur vaterlandische Naturkunde in Wurttemberg 63:1–100.

Manuscript received 10 February 2010, revised 14 March 2011.

2011. The Journal of Arachnology 39:533–536

SHORT COMMUNICATION

Sexual behavior of *Acanthogonatus centralis* (Araneae: Mygalomorphae: Nemesiidae) from Argentina, with some notes on their burrows

Nelson Ferretti[1], **Gabriel Pompozzi**[2], and **Fernando Pérez-Miles**[3]: [1]Centro de estudios parasitológicos y de vectores (CEPAVE) (CCT-CONICET-La Plata), Calle 2 N° 584, (1900) La Plata, Argentina. E-mail: nferretti@conicet.gov.ar; [2]Universidad Nacional del Sur, Dpto. de Biología, Bioquímica y Farmacia, San Juan 670, (8000) Bahía Blanca Argentina; [3]Facultad de Ciencias, Sección Entomología, Iguá 4225, 11400 Montevideo, Uruguay

Abstract. *Acanthogonatus centralis* Goloboff 1995 is a Neotropical nemesiid distributed in hilly zones of central Argentina. The biology of the Nemesiidae is almost unknown. We describe the courtship and mating of *A. centralis* based on eight observed matings (three males and five females). Male courtship involved scratching and beating the ground. These behaviors have not been observed in other mygalomorph spiders and are here described for the first time. After contacting female silk, males stretched the web. Males manipulated their pedipalps and spasmodically beat their legs over the female. The mating position was typical of mygalomorph spiders. Females remained active during copulation by making body jerks and struggling. The body jerks of females could be stimulating the male to renew palpal insertion. In addition to describing this spider family's mating behavior, we also include some notes on their shelters. The tunnel-webs observed in the field had no branches, only one entrance, and a short burrow. Adult males are capable of constructing tunnel-webs, but they are quite different from those of juveniles and females, lacking the short burrow.

Keywords: Neotropical, Argentinean mygalomorph, mating behavior, tunnel-webs

The family Nemesiidae has 41 genera and 342 described species, distributed worldwide (Platnick 2010). These spiders are found across the tropical and subtropical regions of South America, but their biology is almost unknown, with only notes available on a few species mainly distributed throughout Peru, Chile, Argentina, and Uruguay (Goloboff 1995). Most studies on mygalomorph mating behavior and reproductive biology have focused on the Theraphosidae (Shillington & Verrel 1997; Costa & Pérez-Miles 2002; Ferretti & Ferrero 2008). In the Nemesiidae, we could find published behavioral and ecological studies for only three species of *Acanthogonatus*: *A. tacuariensis* (Pérez-Miles & Capocasale 1982) (Costa, as cited by Pérez-Miles & Capocasale 1982; Capocasale & Pérez-Miles 1990) from Uruguay; *A. pissi* (Simon 1889) (Calderón et al. 1979), and *A. franckii* Karsch 1880 (Pinto & Sáiz 1997) from Chile and some aspects of the natural history of six European species of *Nemesia* (Decae 2005). Because of the lack in diversity of mygalomorph species studied, it is imperative to develop an understanding of their reproductive biology. *Acanthogonatus centralis* Goloboff 1995 is a mygalomorph spider commonly found in the hilly areas of central Argentina. However, no natural history data have been published about this species. These are medium-sized nemesiids, both males and females averaging 11.92 ± 1.26 SD mm (n = 10) in total body length, excluding chelicerae and spinnerets. Our goal was to describe the sexual behavior of *A. centralis*, adding some notes about their burrows in the wild and their construction in the laboratory.

We collected five males and five females from the locality of Sierra de la Ventana (38°04′21.3″S, 62°03′02.6″W), Buenos Aires Province, Argentina, in 2007. Voucher specimens from this study were deposited in the collection of the Laboratorio de Zoología de Invertebrados II, Universidad Nacional del Sur, Argentina. We maintained individuals in plastic Petri dishes, with soil as substratum and a patch of wet cotton wool. We used a 12 h light/dark cycle. The room temperature during breeding and experiments was 26.7° ± 1.52° C. The mating arenas, consisting of glass cylindrical containers (19 cm diameter and 10 cm high) with a layer of sand soil, were illuminated with fluorescent light. We made 25 male-female pairings of *A. centralis* in all possible combinations, but we considered only eight of these interactions to be successful examples of courtship behavior resulting in copulation. Males never initiated courtship in the other pairings, and spiders did not make contact. The individuals in a pair were never tested together more than once, and none was used in more than one test on a given day. Each spider was reused one day after the first experiment, but in different combinations. Individuals were randomly assigned to pairs. Encounters were directly observed, recorded with notes and videotaped. We tested the normality and homogeneity of variance of continuous variables using Kolgomorov-Smirnov and Levene tests, respectively. We used the Spearman correlation coefficient (nonparametric test). Mean ± SD values are presented. We performed all statistical analyses using SPSS version 14.0 for Windows (2005).

We recorded eight matings: one male mated twice and two males mated three times, while one female mated three times, another female mated twice, and three females mated one time (n = 3 males, 5 females). When male *A. centralis* engaged in courtship and mated, a common pattern occurred (Fig. 1). In all successful matings males initiated courtship (latency of 59.18 ± 43.3 s) by scratching very rapidly over the substrate surface with the first two pairs of legs. These movements consisted of the male extending his leg forward, touching the substrate, then moving the leg backward over the substrate, removing the soil from in front of the female's burrow and piling it at a distance. This behavior had a mean duration of 1.59 ± 0.69 s (range = 0.95–3.17) and a mean number of 3.87 ± 8.2 scratches (per courtship), n = 8. The male then displayed vigorously, beating the substrate with the first two pairs of legs. These beats consisted of elevating a leg, extending it, and lowering it rapidly to hit the soil, the pattern involving each leg simultaneously. The mean number of beats per courtship was 1.87 ± 3.94, n = 8. The scratching and beating behaviors with the first pair of legs were not observed in *A. tacuariensis* (Costa, as cited by Pérez-Miles & Capocasale 1982) and are described here for the first time for *A. centralis*. Scratching and beating behavior may serve as long-distance male-female communication.

When a male *A. centralis* made contact with the silk threads, he began to stretch the web with the claws of his first pair of legs using brusque, synchronous movements. During the course of this behavior

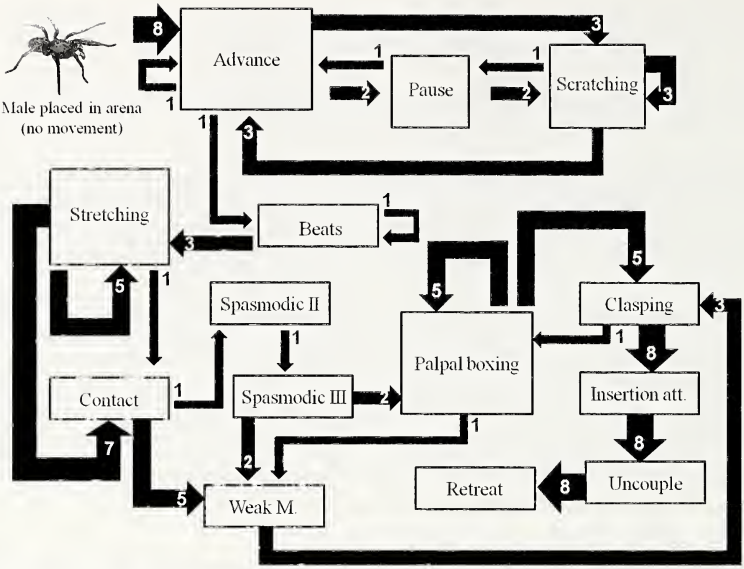


Figure 1.—Ethogram from the eight successful matings showing the courtship and mating pattern of *Acanthogonatus centralis* males. The size of the arrows is proportional to the number of times a behavior was observed.

the male slowly extended legs I downward to contact the web and then flexed them, reaching an angle of 45° between the femur and patella. The mean number of stretches per interaction was 8.5 ± 7.34, $n = 8$. The stretching of the tunnel-web silk also was observed in *A. tacuariensis* (as cited by Pérez-Miles & Capocasale 1982), and this signal could act in short-distance communication. The sequence Substrate Scratching – Silk Stretching is considered to be pre-contact courtship, with a duration of 5.87 ± 5.14 min (range = 1.30–15.16 min, $n = 8$). The female emerged from the tunnel-web after 15.85 ± 13.39 ($n = 8$) sequences of pre-contact behavior. When spiders made contact, the female elevated her body to an angle of almost 90° with the substrate, with her first pair of legs elevated and legs III and IV over the substrate. The male then spasmodically beat independently with its second (1.5 ± 2.77 per courtship) and third pair of legs (4.5 ± 7.17 per courtship), making contact with the female's body and legs. Spasmodic beats consisted of extending the leg and making vigorous backward and forward movements, reaching the legs of the female. Females were passive, but displayed open fangs. Costa (as cited by Pérez-Miles & Capocasale 1982) observed spasmodic beats with legs III in *A. tacuariensis*, but *A. centralis* also beat spasmodically with legs II. The main function of this behavior in *Grammostola* species, where males only make spasmodic beats with legs II, seems to be to relax the female fangs, since it is displayed during the clasping and unclasping of the females' fangs (Costa & Pérez-Miles 2002). This leg-beating behavior might also occur in other families of mygalomorphs, considering how few studies have focused on the sexual behavior of this group of spiders.

Subsequently, the male began palpal boxing (an alternating up and down movement of the palpi or pedipalps), contacting the female's sternum. Simultaneously, the male touched her with very gentle, fast movements, with his first pair of legs located between the female's pedipalps and chelicerae. The second pair of the male's legs touched her carapace between legs II and III. The very fast movements with the male's legs I and II also were reported for *A. tacuariensis* (Costa, as cited by Pérez-Miles & Capocasale 1982) and could also be acting to keep the female in a passive condition. The mean duration of palpal boxing was 7.86 ± 1.97 s (range = 1.4–24.05 s, $n = 97$). This behavior was reported for *A. tacuariensis* (Costa, as cited by Pérez-Miles & Capocasale 1982), but was displayed before contact with the female, whereas in *A. centralis* this behavior always occurred after contact with the female. Male *A. centralis* clasped the females' fangs with the tibial apophyses of legs I. During copulation, the male pushed the female back onto her hind legs and raised her, while still standing with the first pair of legs between the chelicerae and distal portion of the coxa of the pedipalps. The male's second pair of legs enveloped the female's carapace while he pulled her vigorously towards him, so his palpi could approach her genital opening (Fig. 2). Throughout some of the copulation attempts it was possible to see that the female's epigynum was distended, with the anterior and posterior genital lips of the epigastric furrow protruding and parted, resulting in a more exposed genital opening than usual. Only one case of such a protrusion was reported for *T. karschi* (Coyle 1985). For most matings, an angle of 90–100° existed between the male and female cephalothoraxes. The female's pedicel was flexed upward, reaching a cephalothorax-abdomen angle of 60–80°. From this position, the male inserted his embolus into the female's genital opening. The mating position that we observed in *A. centralis* was typical of mygalomorph spiders, with the male positioned in front of the female, but the angle observed was more acute than that found for *A. tacuariensis* (Costa, as cited by Pérez-Miles & Capocasale 1982) and many theraphosids (Jackson & Pollard 1990; Shillington & Verrel 1997; Costa & Pérez-Miles 2002; Ferretti & Ferrero 2008), resembling that described by Coyle 1986 and Coyle & O'Shields 1990 for *Euagrus* species and *T. karschi*. This position seems to result from the vigorous pulling on the female by the male with his second pair of legs. The mean number of insertions was 4.75 ± 3.65 SD, $n = 8$ (range = 2–13),

Figure 2.—*Acanthogonatus centralis* mating. Male clasping the female fangs with legs I, pulling with legs II, and inserting the embolus into the female genital opening. Photo by G. Pompozzi.

and the mean duration of each insertion was 5.29 ± 0.08 SD s, $n = 38$, ranging from 3.33 to 7.85 s. In this phase we observed characteristic body jerks of females before the palpal insertions (4.75 ± 1.70 SD body jerks per mating) made by the high amplitude twitching of all legs and palps. Moreover, the stretching of the male's posterior legs over the substrate resulted in a brusque and quick forward movement of the female body. Males never started the palpal insertions until females made body jerks. The time elapsed between the body jerks decreased with the increased number of this behavioral sequence. The mean duration of the last pre-insertion body jerk of females was 2.38 ± 1.48 s, $n = 8$, while the mean latency of first body jerk of female to the first palpal insertion was 38.29 ± 29.22 s, $n = 8$. We found no relation between the number of body jerks and the number of palpal insertions (Spearman correlation coefficient, $r_s = 0.092$, $P = 0.838$). No significant correlation was found between the latency from the first female body jerk to the first male insertion and the number of insertions (Spearman correlation coefficient, $r_s = 0.232$, $P = 0.658$). In addition, during palpal insertions the male performed repeated vigorous pulsing flexions with the active palpal bulb made by the flexion of the tibia and tarsus of the palp, pulling and twisting the female's abdomen from side to side towards him. The number of palpal insertions by *A. centralis* was variable and similar to that recorded for *A. tacuariensis* (Costa, as cited by Pérez-Miles & Capocasale 1982). Coyle & O'Shields (1990) observed that the vigorous male palpal movements during copulation subsequently twisted the abdomen of females. Moreover, Coyle (1985) observed that palpal movements by male *Microhexura montivaga* Crosby & Bishop 1925 were so vigorous that the female's abdomen was visibly jarred. Subsequently, we observed *A. centralis* females moving their fangs (83.3% of mating), raising and lowering them near the male's carapace, but no bite was registered. The mean duration of copulation was 2.25 ± 1.08 min, $n = 8$. Afterwards, the male unclasped himself from the female, again made spasmodic beats with legs II, started to walk backwards, and then ran forward very quickly in order to escape from the female.

The female role during mating in *A. centralis* was remarkably active, including periods of struggling and body jerks. Females of *Thelechoris karschi* Bösenberg & Lenz 1895 (Dipluridae) occasionally manifest quivering of legs and pedipalps during copulation (Coyle & O'Shields 1990). However, females of the family Theraphosidae usually stay immobile during copulation (Shillington & Verrel 1997; Costa & Pérez-Miles 2002; Bertani et al. 2008; Ferretti & Ferrero 2008); however, struggling behavior was reported for *M. montivaga* and was related to brief couplings and a low number of insertions (Coyle 1985). Males clearly increased the palpal boxing at low latencies (ca. 2 s) between the body jerks of females. Moreover, these body jerks from females may act as a stimulus to start male palpal insertions. In the Lycosidae, *Allocosa brasiliensis* (Petrunkevitch 1910) females made body jerks immediately before each insertion, which could serve as a similar positive signal by females for a new male palpal insertion (A. Peretti pers. comm.).

Male *Acanthogonatus centralis* performed intense courtship both away from and near the tunnel-webs of females, until females left their shelters and copulation took place outside the tunnel-webs. In nature, we always found these mygalomorph spiders under stones in hilly zones where they constructed their tunnel-web shelters. No individuals were observed constructing tunnel-webs in the accumulated earth between stones. Usually, the nemesiids of the genus *Acanthogonatus* live under or between stones and logs, where they construct their tunnel-webs (Capocasale & Pérez-Miles 1990; Pinto & Sáiz 1997). In general, the tunnel-webs of *A.centralis* are similar to those of *A. tacuariensis* (Capocasale & Pérez-Miles 1990) and *A. pissii* (Calderón et al. 1979), but those of *A. centralis* had no branches and only one entrance. These tunnel-webs were horizontal and often were connected to a short burrow. Generally the silk tube occupied the first part of the tunnel-web, with the exception of males, in whose burrows the silk tube was placed at the end of the tunnel-web. We observed only one entrance to the tunnel-webs, and none had branches. Females ($n = 4$) and juveniles constructed burrows behind silk tubes, and juvenile shelters ($n = 3$) appeared more sinuous. The entrance of the tunnel-webs was between 1–1.7 cm in diameter, the silk tubes measured 4–9 cm, and the burrows were 3–7 cm deep. The ability of these spiders to construct a tunnel-web is considered a plesiomorphy and could be a generic level character (Capocasale & Pérez-Miles

1990), although some species of *Acanthogonatus* make tunnel-webs and others live in open burrows (Goloboff 1995). Tunnel-webs could be important in retaining water and reducing the potential loss of it from individuals' bodies in arid habitats (Capocasale & Pérez-Miles 1990). Males ($n = 3$) made silk tubes covered only with debris, with entrances 1.5–2 cm long in soil depressions; the silk tubes measured 5–9.3 cm. Adult male *A. tacuariensis* do not make tunnel-webs and are shorter-lived than the adult females (Capocasale & Pérez-Miles 1990). However, adult male *A. centralis* construct tunnel-webs, lacking the short burrow seen in juveniles and females.

Spider mating in captivity does not appear to be altered when compared to mating behavior in nature (Jackson & Pollard 1990; Bertani et al. 2008), and it seems likely that our observations in the laboratory are typical of *A. centralis* mating behavior in the wild. Many of these behaviors may be homologous with those of the Nemesiidae, but information about many more species is required to make stronger arguments regarding the evolution of courtship and mating behavior in *Acanthogonatus* and related families. Information on courtship and mating behavior of the Mygalomorphae is very important for tracing the evolution of their sexual behavior.

ACKNOWLEDGMENTS

We thank Linden Higgins, Alfredo Peretti, and an anonymous reviewer for many helpful comments on the manuscript. Thanks to Sofía Copperi, Georgina Zapperi, and Mara Maldonado, who helped to collect the specimens. Special thanks to Adriana Ferrero and the Laboratory of Zoology of Invertebrates II for providing spider housing facilities. The senior author has a fellowship from CONICET.

LITERATURE CITED

Bertani, R., C.S. Fukushima & P.I. Da Silva Júnior. 2008. Mating behavior of *Sickius longibulbi* (Araneae, Theraphosidae, Ischnocolinae), a spider that lacks spermathecae. Journal of Arachnology 36:331–335.

Calderón, R., G. Pizarro, C. Rojas, J. Salinas & M. Vivianco. 1979. Observaciones sobre la biología de *Tryssothele pissii* (Simon, 1888) (Araneae, Dipluridae) en el Parque Nacional La Campana. Anales del Museo de Historia Natural de Valparaíso 12:195–205.

Capocasale, M.R. & F. Pérez-Miles. 1990. Behavioural ecology of *Acanthogonatus tacuariensis* (Pérez & Capocasale) (Araneae, Nemesiidae). Studies of Neotropical Fauna and Environment 25:41–47.

Costa, F.G. & F. Pérez-Miles. 2002. Reproductive biology of Uruguayan theraphosids (Araneae, Theraphosidae). Journal of Arachnology 30:571–587.

Coyle, F.A. 1985. Observations on the mating behaviour of the tiny mygalomorph spider, *Microhexura montivaga* Crosby & Bishop (Araneae, Dipluridae). Bulletin of the British Arachnological Society 6:328–330.

Coyle, F.A. 1986. Courtship, mating, and the function of male-specific structures in the mygalomorph spider genus *Euagrus* (Araneae, Dipluridae). Pp. 33–38. *In* Proceedings of the Ninth International Congress of Arachnology, Panama. (W.G. Eberhard, Y.D. Lubin & B.C. Robinson, eds.). Smithsonian Institution Press, Washington, DC.

Coyle, F.A. & T.C. O'Shields. 1990. Courtship and mating behavior of *Thelechoris karschi* (Araneae, Dipluridae), an African funnelweb spider. Journal of Arachnology 18:281–296.

Decae, A.E. 2005. Trapdoor spiders of the genus *Nemesia* Audouin, 1826 on Majorca and Ibiza: taxonomy, distribution and behaviour (Araneae, Mygalomorphae, Nemesiidae). Bulletin of the British Arachnological Society 13;145–168.

Ferretti, N. & A. Ferrero. 2008. Courtship and mating behavior of *Grammostola schulzei* (Schmidt 1994) (Araneae, Theraphosidae), a burrowing tarantula from Argentina. Journal of Arachnology 36:480–483.

Goloboff, P.A. 1995. A revision of the South American spiders of the family Nemesiidae (Araneae, Mygalomorphae). Part I: species from Peru, Chile, Argentina and Uruguay. Bulletin of the American Museum of Natural History 224:1–189.

Jackson, R.R. & S.D. Pollard. 1990. Intraspecific interactions and the function of courtship in mygalomorph spiders: a study of *Porrothele antipodiana* (Araneae, Hexathelidae) and a literature review. New Zealand Journal of Zoology 17:499–526.

Pérez-Miles, F. & R. Capocasale. 1982. Hallazgo de una tercera especie del género *Pycnothelopsis*: *Pycnothelopsis tacuariensis* sp. nov. (Araneae, Pycnothelidae). Comunicaciones Zoológicas del Museo de Historia Natural de Montevideo 9(147):1–7.

Pinto, C. & F. Sáiz. 1997. Uso del recurso trófico por parte de *Acanthogonatus franckii* Karsch, 1880 (Araneae: Nemesiidae) en el bosque esclerófilo del Parque Nacional "La Campana", Chile central. Revista Chilena de Entomología 24:45–59.

Platnick, N.I. 2010. The World Spider Catalog, Version 11.0. American Museum of Natural History, New York. Online at http://research.amnh.org/entomology/spiders/catalog/index.html

Shillington, C. & P. Verrell. 1997. Sexual strategies of a North American "tarantula" (Araneae, Theraphosidae). Ethology 103:588–598.

Manuscript received 3 August 2009, revised 27 March 2011.

2011. The Journal of Arachnology 39:537–540

SHORT COMMUNICATION

The composition of spider assemblages varies along reproductive and architectural gradients in the shrub *Byrsonima intermedia* (Malpighiaceae)

Augusto Cesar de Aquino Ribas: Graduate Program in Ecology and Conservation, Universidade Federal de Mato Grosso do Sul, Campo Grande, MS, Brazil. E-mail: ribas.aca@gmail.com

Antonio Domingos Brescovit: Laboratório de Artrópodes, Instituto Butantan, Av. Vital Brasil, 1500, Butantã, São Paulo, SP, Brazil

Josué Raizer: School of Biological and Environmental Sciences, Universidade Federal da Grande Dourados, Dourados, MS, Brazil

Abstract. The presence of buds, flowers, and fruits increases structural complexity in plants, but can also attract potential prey for predators, thus determining faunistic composition. To understand how a spider assemblage living in the shrub *Byrsonima intermedia* (Malpighiaceae) varies with habitat structure in terms of reproductive elements and height of plant, we collected spider specimens and measured bud, flower, fruit, and leaf masses of 44 plants, as well as their height. Spider family composition was found to depend on habitat structure, following a pattern of family turnover occurring along gradients of reproductive plant elements and height, regardless of plant biomass. Theridiidae occurred in samples with the major proportions of buds and flowers, while Oxyopidae occurred only in samples with major proportions of fruits. Multiple linear regression revealed the strong relation between the composition in reproductive plant elements and the composition in families of spiders and a relation between shrub height and spider family composition. These results help us to understand the temporal dynamics between structural complexity of vegetation and spider assemblages, because during plant phenology the proportions of reproductive elements are also varying.

Keywords: Araneae, assemblage composition, assemblage diversity, habitat structure, habitat heterogeneity, reproductive phenology

The influence of plant structural traits on microhabitat selection has been demonstrated for spiders around the world. The spiders' preferences for particular microhabitats result in variation of spider diversity related to both the structure of vegetative parts (Halaj et al. 2000; Souza 2005) and the presence of reproductive structures (Souza & Modena 2004; Souza & Martins 2004).

Inflorescence-bearing branches are structurally distinct from vegetative branches and may constitute microhabitats that offer a range of attractive traits for spiders. Floral structures may provide refuge from predators and harsh environmental conditions, facilitating camouflaging for prey capture and serving as breeding sites (Johnson 1995). Abundance of potential prey for spiders is high in buds and flowers, as these structures are often visited by herbivores and pollinating insects (Louda 1982). Furthermore, fruits attract insects and may depend on these to complete their life cycles (e.g., Kolesik et al. 2005; Burkhardt et al. 2009). Plant phenological variation is therefore expected to determine variations in the structure of spider assemblages.

The presence and succession of reproductive elements of plants mask the effects of plant structural complexity on spider diversity, because reproductive structures not only modify plant architecture (by changing biomass spatial arrangement), but also amplify the local prey availability, being attractive to spiders for many reasons (e.g., Finke & Denno 2006; Schmidt & Rypstra 2010).

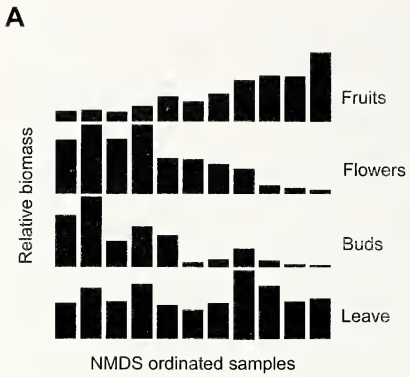
We desired to know if the relative amount of each reproductive element (buds, flowers and fruits), height (plant architecture), and biomass (habitat size) of the shrub *Byrsonima intermedia* A. Juss (Malpighiaceae) might explain variation in the composition of spider assemblages. The architecture of this shrub species varies with height (Oliveira et al. 2007), because the taller the specimen, the further apart its branches are arranged, facilitating the construction of wider webs.

Data were collected from an area of the Brazilian savanna ("cerrado stricto sensu") in Campo Grande, Mato Grosso do Sul, southwestern Brazil (Embrapa Gado de Corte, 20°26′36.6″S, 54°43′30.6″W). The area, now undergoing regeneration, harbors a large number of *B. intermedia* specimens with asynchronic flowering. The species has entomophilous flowers that last for one day on average and develop into a drupe (Oliveira et al. 2007).

From 17 October to 4 December 2008, a total of 44 shrubs (typically six each week) was sampled. To randomize the choice of shrubs, the posts of an adjoining fence were numbered. A fencepost and a perpendicular distance in meters (integers from 0 to 100) were then chosen by draw. Fencepost and distance determined a spot from which the nearest *B. intermedia* shrub was selected. While uncut, the plants were individually wrapped in plastic bags of 100 l capacity, then cut at ground level using pruning shears before taken to the laboratory, where each shrub (mean height = 1.24 m, SD = 0.25; biomass = 461.2 g, SD = 252.3) was inspected for the presence of arthropods. The spiders thus collected were stored for identification at the family level. Voucher specimens were deposited in the Arachnida collection of Instituto Butantan of São Paulo, Brazil.

After removal of the arthropods, all the buds, flowers, fruits, and leaves from each shrub were collected, and the fresh mass of each of these types of structure was weighed using a balance of 0.01 g precision right after the removal of the arthropods in the same day of sampling.

As *B. intermedia* is a species with an asynchronous flowering period (Filho & Lomônaco 2006). The 44 plant specimens were randomly grouped, taking into account the frequency of spider families, mean plant height, and total biomass of shrubs, leaves, buds, flowers, and fruits, resulting in 11 samples of four specimens each, allowing us to make ordinations of the variables without losing the relation between them.



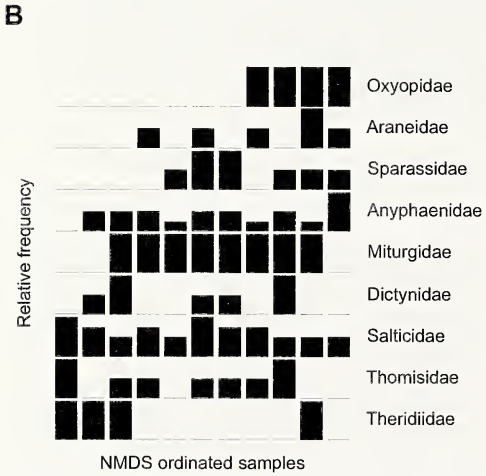
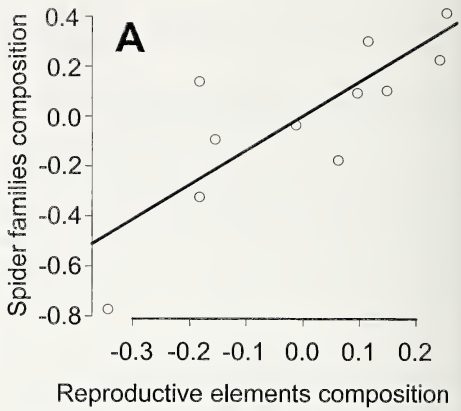


Figure 1.—Ordinations of the samples by non-metric multidimensional scaling (NMDS). (A) Phenological variation: ordination obtained using relative biomass of leaves, buds, flowers and fruits in *Byrsonima intermedia* specimens (Malpighiaceae). (B) Spider family composition: ordination obtained using relative frequency of the spider families.



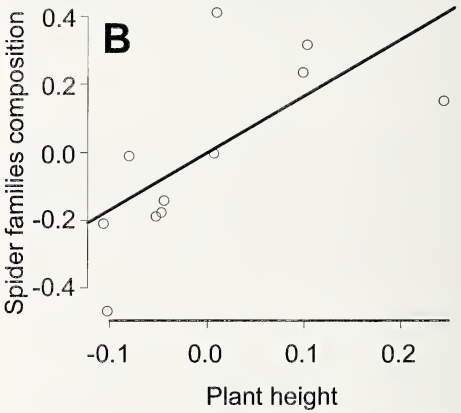


Figure 2.—Partial regression plots of the multiple regression model. NMDS scores for relative frequencies of spider families are values of the dependent variable and NMDS scores of relative masses of reproductive elements (A) and height of *Byrsonima intermedia* (Malpighiaceae) shrubs (B) are the independent variables. Lines represent the linear function obtained in the multiple regression model.

Ordination by non-metric multidimensional scaling (NMDS) was employed to represent the variation in relative amounts of leaves, buds, flowers, and fruits across plant samples. We considered the relative biomass of vegetative structures (leaves) and reproductive structures (buds, flowers, and fruits), employing a Bray–Curtis dissimilarity matrix for this ordination. NMDS was also used to represent spider family composition. A Bray–Curtis dissimilarity matrix based on relative frequencies was also employed for this purpose.

A multiple linear regression model was used to evaluate the effects of reproductive plant elements (NMDS scores), height, and biomass on the diversity (Shannon index) and composition (NMDS scores) of spider families. R software (R Development Core Team 2010) was used for data analysis. The vegan software package (Oksansen et al. 2010) was additionally employed for diversity calculations and for ordinations.

Ordination of *B. intermedia* samples using the relative mass of leaves, buds, flowers, and fruits using NMDS ($n = 11$, $R^2 = 0.94$) revealed variation in composition of the reproductive elements (Fig. 1A). Samples with more buds remained on the left in the

gradient of ordination, while flowers decreased and fruits increased along this gradient. Leaves were abundant in all samples throughout this gradient, irrespective of reproductive elements.

A total of 195 spiders from nine families was collected from 44 shrubs. Salticidae (62 specimens), Anyphaenidae (33), and Thomisidae (21) were the most abundant families. A mean Shannon's index of 1.49 was found for family diversity, ranging from 0.67 to 1.86 for the 11 samples and varying randomly with reproductive plant elements, height, and biomass in a multiple regression model ($n = 11$; $F = 2.63$; $R^2 = 0.68$; $P = 0.35$).

Sample ordination by NMDS ($n = 11$; $R^2 = 0.73$) using relative frequencies of spider occurrence, revealed a gradient in spider family composition (Fig. 1B). Spiders of the family Salticidae were found throughout this gradient; Theridiidae and Thomisidae were more likely to occur at the beginning of the gradient; Araneidae and Oxyopidae, at the end. Other families occurred in intermediate portions of the gradient.

In a multiple regression model ($n = 11$; $R^2 = 0.68$; $F = 4.79$; $P = 0.04$), NMDS scores for spider family composition varied as a linear function of NMDS scores for composition of reproductive plant elements ($b = 1.68$; $t = 2.77$; $P = 0.03$) and height ($b = 0.38$; $t = 3.46$; $P = 0.01$), but not of biomass ($P = 0.573$). This finding reveals that, regardless of aboveground biomass, *B. intermedia*'s height and composition of reproductive elements explained 68% of the variation in the spider assemblage (Fig. 2).

Although associations between spiders and certain types of flowers and fruits have been described in the literature (Souza & Modena 2004; Souza & Martins 2004), the present study is, to our knowledge, the first to demonstrate how the composition of a spider assemblage varies with a quantitative measure of composition of the reproductive elements, irrespective of total plant biomass. Since variation in plant architecture as a function of size influences habitat complexity (Souza & Martins 2004; Faria & Lima 2008), this investigation evaluated the isolated effect of architecture by measuring shrub height and disregarding the variation due to biomass, which was achieved by taking into account the multiple regression model. Taller shrubs have more branches and these are more spread out, whereas biomass represents the amount of habitat available for spiders.

Several studies have demonstrated associations between plants and spiders, most often of single species (Johnson 1995; Romero & Vasconcellos-Neto 2005), but also of multiple species (Halaj et al. 2000; Raizer & Amaral 2001; Souza & Martins 2004). These studies corroborate the assumption that habitat architectural traits define the composition of spider species.

Each component of the phenology of *B. intermedia* can represent either an increase or a decrease in spider abundance and diversity (Romero & Vasconcellos-Neto 2005). In the present study, the added effects of leaf, bud, flower, and fruit biomass on spider occurrence revealed a pattern of family turnover in which Theridiidae occured in samples with the major proportions of buds and flowers, while Oxyopidae occurred only in samples with major proportions of fruits. This pattern suggests that niche partitioning is dependent on the reproductive phenology of *B. intermedia*, more specifically dependent on the composition of reproductive elements.

This response seen in the structure of the spider assemblage possibly influences the indirect interactions between spiders and reproductive success (e.g., fruit-set and seed set) of plants (Louda 1982; Goncalves-Souza et al. 2008; Romero et al. 2008). Different components of the reproductive stage of plants are expected to have different effects on the attraction of spiders of each family (Souza & Martins 2004; Romero & Vasconcellos-Neto 2005), and general patterns such as those described in this study are additive responses resulting from these family-level patterns. Not only knowledge of the effect of each reproductive component of plant, but also of the interaction between these components (e.g., decreased plant cross pollination due to spiders predating on pollinators and fruit protection due to predation on herbivores), is necessary to understand the structure of a spider assemblage and help to predict potential responses to indirect interactions between spiders and plants (Wootton 2002). It can be concluded that spider composition depends on habitat structure, with a pattern of family turnover occurring along gradients of composition of reproductive elements and height, irrespective of plant biomass.

ACKNOWLEDGMENTS

We thank F.O. Roque, J.C. Voltolini, S. Pekar and two anonymous reviewers for their helpful suggestions and comments. V.L. Landeiro provided R functions for the graphs in Fig. 1. This research was supported by the FUNDECT, a governmental foundation of Mato Grosso do Sul State (process 23/200.327/2008 and 23/200.384/2008) and by Conselho Nacional do Desenvolvimento Científico e Tecnológico (CNPq grant 301776/2004-0 to ADB).

LITERATURE CITED

Burkhardt, A., L.F. Delph & G. Bernasconi. 2009. Benefits and costs to pollinating, seed-eating insects: the effect of flower size and fruit abortion on larval performance. Oecologia 161:87–98.

Faria, R.R. & T.N. Lima. 2008. Spiders associated with *Psychotria carthagenensis* Jacquin. (Rubiaceae): vegetative branches versus inflorescences, and the influence of *Crematogaster* sp. (Hymenoptera, Formicidae), in South-Pantanal, Brazil. Brazilian Journal of Biology 68:229–232.

Filho, L.C.R. & C. Lomônaco. 2006. Variações fenotípicas em subpopulações de *Davilla elliptica* A. St.-Hil. (Dilleniaceae) e *Byrsonima intermedia* A. Juss. (Malpighiaceae) em uma área de transição cerrado-vereda. Acta Botanica Brasiliense 20:719–725.

Finke, D.L. & R.F. Denno. 2006. Spatial refuge from intraguild predation: implications for prey suppression and trophic cascades. Oecologia 149:265–275.

Goncalves-Souza, T., P.M. Omena, J.C. Souza & G.Q. Romero. 2008. Trait-mediated effects on flowers: artificial spiders deceive pollinators and decrease plant fitness. Ecology 89:2407–2413.

Halaj, J., D.W. Ross & A.R. Moldenke. 2000. Importance of habitat structure to the arthropod food-web in Douglas-fir canopies. Oikos 90:139–152.

Höfer, H. & A.D. Brescovit. 2001. Species and guild structure of a Neotropical spider assemblage (Araneae) from Reserva Ducke, Amazonas, Brazil. Andrias 15:99–119.

Johnson, S.R. 1995. Observations of habitat use by *Sarinda hentzi* (Araneae, Salticidae) in Northeastern Kansas. Journal of Arachnology 23:71–74.

Kolesik, P., R.J. Adair & G. Eick. 2005. Nine new species of *Dasineura* (Diptera: Cecidomyiidae) from flowers of Australian *Acacia* (Mimosaceae). Systematic Entomology 30:454–479.

Louda, S.M. 1982. Inflorescence spiders: a cost/benefit analysis for the host plant, *Haplopappus venetus* Blake (Asteraceae). Oecologia 55:185–191.

Oksanen, J., F.G. Blanchet, R. Kindt, P. Legendre, R.B. O'Hara, G.L. Simpson, P. Solymos, M.H.H. Stevens & H. Wagner. 2010. Vegan: Community Ecology Package. R package version 1.17-4. Online at http://www.R-project.org

Oliveira, M.I.B., C.A. Polido, L.C. Costa & W.S. Fava. 2007. Sistema reprodutivo e polinização de *Byrsonima intermedia* A. Juss. (Malpighiaceae) em Mato Grosso do Sul, Brasil. Revista Brasileira Biociências 5:756–758.

R Development Core Team. 2010. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. Online at http://www.R-project.org

Raizer, J. & M.E.C. Amaral. 2001. Does the structural complexity of aquatic macrophytes explain the diversity of associated spider assemblages? Journal of Arachnology 29:227–237.

Romero, G.Q., J.C. Souza & J. Vasconcellos-Neto. 2008. Anti-herbivore protection by mutualistic spiders and the role of plant glandular trichomes. Ecology 89:3105–3115.

Romero, G.Q. & J. Vasconcellos-Neto. 2005. The effects of plant structure on the spatial and microspatial distribution of a bromeliad-living jumping spider (Salticidae). Journal of Animal Ecology 74:12–21.

Schmidt, J.M. & A.L. Rypstra. 2010. Opportunistic predator prefers habitat complexity that exposes prey while reducing cannibalism and intraguild encounters. Oecologia 164:899–910.

Souza, A.L.T. 2005. Foliage density of branches and distribution of plant-dwelling spiders. Biotropica 37:416–420.

Souza, A.L.T. & R.P. Martins. 2004. Distribution of plant-dwelling spiders: inflorescences versus vegetative branches. Austral Ecology 29:342–349.

Souza, A.L.T. & E.S. Modena. 2004. Distribution of spiders on different types of inflorescences in the Brazilian Pantanal. Journal of Arachnology 32:345–348.

Wootton, J.T. 2002. Indirect effects in complex ecosystems: recent progress and future challenges. Journal of Sea Research 48: 157–172.

Manuscript received 19 December 2010, revised 18 August 2011.

2011. The Journal of Arachnology 39:541–542

INSTRUCTIONS TO AUTHORS
(instructions last revised October 2011)

General: The *Journal of Arachnology* publishes scientific articles reporting novel and significant observations and data regarding any aspect of the biology of arachnid groups. Feature articles and short communications must be scientifically rigorous and report substantially new information. Submissions that are overly narrow in focus (e.g., local faunal lists, descriptions of a second sex or of a single species without additional discussion of the significance of this information), have poorly substantiated observational data, or that present no new information will not be considered. Book reviews will not be published.

Manuscripts must be in English and should be prepared in general accordance with the current edition of the *Council of Biological Editors Style Manual* unless instructed otherwise below. Use the active voice throughout. Authors should consult a recent issue of the *Journal of Arachnology* for additional points of style. Manuscripts longer than three printed journal pages (12 or more double-spaced manuscript pages) should be prepared as Feature Articles, shorter papers as Short Communications. Review Articles will be published from time to time. Suggestions for review articles may be sent to the Managing Editor. Unsolicited review articles are also welcomed. All review articles will be subject to the same review process as other submissions.

Submission: Submissions must be sent electronically in Microsoft Word format (not pdf) to the Managing Editor of the *Journal of Arachnology*: **Douglass H. Morse, Managing Editor, Hermon Carey Bumpus Professor of Biology Emeritus, Department of Ecology & Evolutionary Biology, Box G-W, Brown University, Providence, RI 02912 USA** [Telephone: 401-863-3152; Fax: 401-863-2166; E-mail: d_morse@brown.edu]. The entire manuscript should be submitted as one Word document. Figures should be at low resolution for the initial review.

The Managing Editor will acknowledge receipt of the manuscript, assign it a manuscript number and forward it to an Associate Editor for the review process. Correspondence relating to manuscripts should be directed to the Associate Editor and should include the manuscript number. If the manuscript is accepted, the author will be asked to submit the final copy electronically to the Associate Editor. Submission of final illustrations is detailed below. Authors are expected to return revisions promptly. Revised manuscripts that are not returned in a reasonable time period (no longer than six months for minor revisions and one year for major revisions) will be considered new submissions.

Voucher Specimens: Specimens of species used in your research should be deposited in a recognized scientific institution. All type material must be deposited in a recognized collection/institution.

FEATURE ARTICLES

Title page.—The title page includes the complete name, address, and telephone number of the corresponding author; a FAX number and electronic mail address if available; the title in sentence case, with no more than 65 characters and spaces per line in the title; each author's name and address; and the running head.

Running head.—The author's surname(s) and an abbreviated title should be typed in all capital letters and must not exceed 60 characters and spaces. The running head should be placed near the top of the title page.

Abstract.—Length: ≤ 250 words for Feature Articles; ≤ 150 words for Short Communications.

Keywords.—Give 3–5 appropriate keywords or phrases following the abstract. Keywords should not duplicate words in the title.

Text.—Double-space text, tables, legends, etc. throughout. Three levels of heads are used.

- The first level (METHODS, RESULTS, etc.) is typed in capitals and centered on a separate line.
- The second level head begins a paragraph with an indent and is separated from the text by a period and a dash.
- The third level may or may not begin a paragraph but is italicized and separated from the text by a colon.

Use only the metric system unless quoting text or referencing collection data. If English measurements are used when referencing collection data, then metric equivalents should also be included parenthetically. All decimal fractions are indicated by a period (e.g., −0.123). Include geographic coordinates for collecting locales if possible.

Citation of references in the text: Cite only papers already published or in press. Include within parentheses the surname of the author followed by the date of publication. A comma separates multiple citations by the same author(s) and a semicolon separates citations by different authors, e.g., (Smith 1970), (Jones 1988; Smith 1993), (Smith & Jones 1986, 1987; Jones et al. 1989). Include a letter of permission from any person who is cited as providing unpublished data in the form of a personal communication.

Citation of taxa in the text: Include the complete taxonomic citation (author & year) for each arachnid taxon when it first appears in the abstract and text proper. For Araneae, this information can be found online at http://research.amnh.org/iz/spiders/catalog/INTRO3.html. For example, *Araneus diadematus* Clerck 1757. Citations for scorpions can be found in the *Catalog of the Scorpions of the World (1758–1998)* by V. Fet, W.D. Sissom, G. Lowe & M.E. Braunwalder. Citations for pseudoscorpions can be found at http://www.museum.wa.gov.au/arachnids/pseudoscorpions. Citations for some species of Opiliones can be found in the *Annotated Catalogue of the Laniatores of the New World (Arachnida, Opiliones)* by A.B. Kury. Citations for other arachnid orders can be found in *Catalogue of the Smaller Arachnid Orders of the World* by M.S. Harvey.

Literature Cited section.—Use the following style and formatting exactly as illustrated; include the full unabbre-

viated journal title. Personal web pages should not be included in Literature Cited. These can be cited within the text as (John Doe, pers. website) without the URL. Institutional websites may be included in Literature Cited.

Carico, J.E. 1993. Trechaleidae: a "new" American spider family. Pp. 305. *In* Proceedings of the Ninth International Congress of Arachnology, Panama 1983. (W.G. Eberhard, Y.D. Lubin & B.C. Robinson, eds.). Smithsonian Institution Press, Washington, D.C.

Huber, B.A. & W.G. Eberhard. 1997. Courtship, copulation, and genital mechanics in *Physocyclus globosus* (Araneae, Pholcidae). Canadian Journal of Zoology 74:905–918.

Krafft, B. 1982. The significance and complexity of communication in spiders. Pp. 15–66. *In* Spider Communication: Mechanisms and Ecological Significance. (P.N. Witt & J.S. Rovner, eds.). Princeton University Press, Princeton, New Jersey.

Platnick, N.I. 2011. The World Spider Catalog, Version 12.0. American Museum of Natural History, New York. Online at http://research.amnh.org/iz/spiders/catalog/

Roewer, C.F. 1954. Katalog der Araneae, Volume 2a. Institut Royal des Sciences Naturelles de Belgique, Bruxelles.

Footnotes.—Footnotes are permitted only on the first printed page to indicate current address or other information concerning the author. All footnotes are placed together on a separate manuscript page. Tables and figures may not have footnotes.

Taxonomic articles.—Consult a recent taxonomic article in the *Journal of Arachnology* for style or contact the Subject Editor for Taxonomy and Systematics. Papers containing original descriptions of focal arachnid taxa should be listed in the Literature Cited section.

Tables.—Each table, with the legend above, should be placed on a separate manuscript page. Only horizontal lines (no more than three) should be included. Tables may not have footnotes; instead, include all information in the legend.

Illustrations.—Original illustrations should be sent electronically when the manuscript is submitted, preferably in tiff or jpeg format. Distribution maps should be considered figures and numbered consecutively with other figures. (Authors wishing to submit figures as hard copies should contact the Editor-in-Chief for specifications.) At the submission and review stages, the resolution standards should be low as long as editors and reviewers can view figures effectively. Final illustrations must be submitted to the Editor-in-Chief, typically by e-mail or on a CD, to ensure that the electronic versions meet publication standards and that they match the printed copy. All figures should be at least 4 inches wide, but no larger than a sheet of letter-size paper with 1-inch margins all around. The resolution should be at least 300 dpi (or ppi) for halftone or color figures and 1200 dpi for line drawings. A Guide to the Digital Art Specs for Allen Press is posted online at: http://allenpress.com/system/files/pdfs/library/apmk_digital_art.pdf. Color plates can be printed, but the author must assume the full cost paid in advance, currently about $1250 US per color plate. Alternatively, an author can opt to have a figure printed in black and white, but for $105/page have that figure appear in color in the online version of the journal. Most figures will be reduced to single-column width (9 cm, 3.5 inches), but large plates can be printed up to two-columns width (18 cm, 7 inches).

Address all questions concerning illustrations to the Editor-in-Chief of the *Journal of Arachnology*: **Robert B. Suter, *Editor-In-Chief,* Biology Department, Vassar College, 124 Raymond Ave., Poughkeepsie, NY 12604-0731, USA** [*Telephone:* 845-437-7421; *FAX:* 845-437-7315; *E-mail:* suter@vassar.edu]

Legends for illustrations should be placed together on the same page(s) and also with each illustration. Each plate must have only one legend, as indicated below:

Figures 1–4. *A-us x-us*, male from Timbuktu. 1, Left leg; 2, Right chelicera; 3, Dorsal aspect of genitalia; 4, Ventral aspect of abdomen. Scale = 1.0 mm.

The following alternate Figure numbering is also acceptable:

Figures 1a–e. *A-us x-us*, male from Timbuktu. a. Left leg; b. Right chelicerae; c. Dorsal aspect of genitalia; d. Ventral aspect of abdomen. Scale = 1.0 mm.

Assemble manuscript.—The manuscript should appear in separate sections or pages in the following sequence: title page, abstract, text, footnotes, tables with legends, figure legends, figures. Send entire manuscript, including figures, as one Microsoft Word document. If figures or plates are large, please separate them from the text and send them as a pdf or jpg file.

Page charges, proofs and reprints.—Page charges are voluntary, but non-members of AAS are strongly encouraged to pay in full or in part for their article ($75 / journal page). The author will be charged for changes made in the proof pages. Hard copy or pdf reprints are available only from Allen Press and should be ordered when the author receives the proof pages. Allen Press will not accept reprint orders after the paper is published. The *Journal of Arachnology* also is available through www.bioone.org and www.jstor.org. Therefore, you can download the PDF version of your article from one of these sites if you or your institution is a member. PDFs of articles older than one year will be made freely available from the AAS website.

SHORT COMMUNICATIONS

Short Communications are usually limited to three journal pages, including tables and figures (11 or fewer double-spaced manuscript pages including Literature Cited; no more than 2 small figures or tables). Internal headings (METHODS, RESULTS, etc.) are omitted. Short communications must include an abstract and keywords.

COVER ARTWORK

Authors are encouraged to send quality photographs (preferably in color) to the editor-in-chief to be considered for use on the cover. Images should be at least 300 dpi.

CONTENTS

Journal of Arachnology

Volume 39 Number 3

Feature Articles

Short Communications

APRIL2013
RIGHT
24ColorCard